The phenology of seaward migration of juvenile brown trout (Salmo trutta) in two European populations

WINTER, EMILY,ROSE

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by

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Abstract

Brown trout (*Salmo trutta*) exhibit facultative partial migration and the factors regulating spring downstream smolt migrations have been well documented in many river systems. Comparatively few studies have investigated movement outside the typical smolt migration period, but recent evidence supports the existence of an alternative autumn downstream migratory phenotype. This study is the first to provide a direct comparison of juvenile autumn downstream migration between two populations. The phenology of downstream migration of wild juvenile trout was examined using passive integrated transponder (PIT) telemetry over an eight month period in two European rivers; the River Deerness, England, and the River Villestrup, Denmark, exhibiting contrasting proximity to the marine environment. Additionally on the Deerness, indices of trout population dynamics were monitored using repeat sample and mark-recapture techniques. Site fidelity was strong (83%) for Deerness trout in summer 2014, but a large degree of local redistribution was evident by March 2015. The incidence of autumn-winter seaward migration was greater in the Deerness (46 % of migrating juveniles detected prior to spring smoltification) than the Villestrup (25 %). In both systems, the probability of migration was positively correlated with water level. While autumn and spring downstream migrants did not differ in size at the time of tagging in either system, evidence that spring migrants were of better condition, travelled faster (autumn: 11.0 km day^{-1}; spring: 24.3 km day^{-1}) and were more likely to leave the Deerness than autumn migrants suggests autumn and spring migrant conspecifics responded to different behavioural motivations. Variation in migration timing and overwintering habitat use could have ecological consequences relating to trophic cascades. Further investigation into the sex of autumn migrant juveniles, as well as the temporal and geographical variability in the incidence and fitness consequences of autumn migration by juvenile trout would be beneficial to salmonid population management.

Contents

Declaration

I, **Emily Rose Winter**, hereby declare that this thesis entitled:

'The phenology of seaward migration of juvenile brown trout (*Salmo trutta*) in two European populations'

is, to the best of my knowledge, a presentation of my own original work and that no work done by any other person or group is included, except where due reference is given in the text. I have acknowledged any sources of help with written work or field work in my acknowledgements.

Statement of copyright

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Chapter 1: General Introduction

Movements of organisms play a fundamental role in the evolution and diversity of life, by determining the structure and dynamics of populations, communities and ecosystems. Intraspecific variation in behaviour, both between populations and between individuals of the same population, is common across a wealth of taxa, and can be said to result from complex interactions between genetic diversity and environmental variability (Chapman *et al.* 2011). Populations and individual organisms differ in their innate predispositions and experiences that instil learning, which can cause variations in traits, such as aggressiveness, activity and risk-taking (Mery & Burns, 2010). Plasticity has been documented for a wide range of behaviours across many animal species , from the variation in foraging activity of harvester ants, *Pogonomyrmex barbatus* (Beverly *et al.* 2009) to the multiple mating strategies of male bighorn sheep, *Ovis canadensis* (Hogg, 1984). In particular, increasing research attention has been directed to the remarkable diversity of migration patterns seen within many animal species. Many studies focus on avian behaviour (e.g. Lundberg, 1988; Alerstam & Hedenstrom, 1998), although numerous others document huge variability in fish, such as in anadromous salmonids (e.g. Klemetsen *et al.* 2003; Dodson *et al.* 2013). This introductory chapter reviews patterns of migratory variability, with particular reference to salmonids and the brown trout, *Salmo trutta*, and discusses areas of ambiguity which would benefit from further investigation.

1.1. DEFINING MIGRATION, ITS EVOLUTION AND ITS VARIATION

The term 'migration' has been applied to wide array of movement types and has been defined on many occasions, for example Baker (1978) described, in general, 'the act of moving from one spatial unit to another', and Endler (1977) proposed, more specifically, 'the relatively long-distance movements made by large numbers of individuals in approximately the same direction at approximately the same time ... usually followed by a regular return migration'. This is in contrast to Endler's (1977) definition of dispersal, given as 'the roughly random and non-directional small-scale movements made by individuals rather than by groups, continuously rather than periodically.' Migration has demanded further explanation, with Dingle (1996) labelling it an undistracted movement between different habitats, accompanied by distinct behaviours of departure and arrival, while Lucas

and Baras (2001) stressed occurrence at specific life cycle stages. Certain conditions, however, such as those proposed by Lucas and Baras (2001), seem to exclude some claimed migratory movement types that occur at high frequency, such as the diel vertical movements of zooplankton (Hansson & Hylander, 2009) and the weekly 'drinking' journeys of Fowler's toads, *Bufo fowleri* (Stille, 1952; Baker, 1978). It is clear definitions of migration and dispersal do not demand binary explanations and, hence, when analysing the variability of migration behaviour, one should be cautious of both broad and restrictive definitions.

The majority of organismal movements occur at a small scale relative to the geographic range of the species, within a home range that provides sufficient resources for survival during distinct time periods (Dingle, 1996). One can ask, therefore, why an organism should choose to migrate between multiple habitats or home ranges. To answer this question, the contribution of each habitat to an organism's evolutionary fitness, as well as the costs associated with movement between the habitats, should be considered (Gross, 1987). A simplistic measure of fitness is given by an organism's net reproductive rate (R_0), quantified by the lifetime summation of the product of an individual's probability of survival to a reproductive age (l_x) with its fecundity/fertility and breeding success (b_x) at age x (Gross, 1987; Jonsson & Jonsson, 1993):

$$R_0 = \sum l_x b_x$$

Clearly, if the reproductive rate of migrant phenotypes that make use of multiple habitats outweighs that of residents in a single habitat, migrants will be evolutionarily favoured. In order to offer explanation to the evolutionary origin of migration, a number of selective pressures have been theorised, including inter- and intraspecific competition, thermal intolerances to seasonality, a seasonal lack of resource or energy availability, and predator abundance (Cox, 1985; Chapman *et al.* 2011). For example, competition-avoidance is apparent for the density-dependent uphill migrations of red deer, *Cervus elaphus*, (Mysterud *et al.* 2011), whereas the migratory tendency of tropical white-ruffed manakins, *Corapipo altera,* is enhanced by an increased frequency of forage-limiting storms (Boyle *et al.* 2010). Instead, the size-dependent migration of bream, *Abramis brama*, is believed to be due to the vulnerability of small individuals to predation (Skov *et al.* 2010). In diadromous fishes (those that migrate between fresh and seawater habitats), such as many of the family Salmonidae, differences in growth opportunities, influenced by habitat

productivity, are key to promoting their movement. For example, anadromous fish (those that reproduce in freshwater but migrate to the ocean for growth and maturation) are common in northern temperate latitudes, where ocean productivity exceeds that of freshwater (Hendry *et al.* 2004). Ultimately, higher marine growth rates, compared to those in natal rivers and streams, facilitate larger sizes-at-age, greater energy stores and enhanced reproductive success, particularly for females (Hendry *et al.* 2004).

Migration is naturally a plastic trait, and variability can take several forms, such as the distance travelled, direction or pathway, threshold of migration tendency and phenology (Baker 1978; Dingle, 1996). The blackcap warbler, *Sylvia atricapilla*, provides a well-studied example of a bird species whose central European populations differ in their migration routes and wintering destinations. Those breeding in the east migrate south-east, wintering mostly in eastern Africa, while western populations migrate west to overwinter in the British Isles or south-west to Spain or adjacent North Africa (Berthold, 1988). Populations of the same species can also differ in their migration tendency. For example, some populations of the milkweed bug, *Oncopeltus fasciatus*, migrate long distances from sub-tropical refuges to North America each spring, while other populations are comparatively sedentary in Central America, moving only between local milkweed patches and breeding throughout the year (Dingle, 1996). Intrapopulation variation in migration behaviour is known as differential migration, when it is known that all individuals in the population migrate (Lundberg, 1988; Dingle, 1996). Often, populations are segregated in their migration characteristics by sex or age, for example females of the dark-eyed junco, *Junco hyemalis*, migrate further and winter to the south of males (Holberton & Able, 2000), while juvenile magnolia warblers, *Dendroica magnolia,* precede adults during their autumn migration to the Neotropics (Woodrey & Chandler, 1997). Additionally, male roe deer, *Capreolus capreolus*, migrate earlier in spring and significantly later in autumn than females, and as a result spend longer in their European summer breeding ranges (Cagnacci *et al.* 2011). A variety of factors may lead to observed sex- or age-specific differences, including developmental constraints and/or reproductive motivations, giving insight into the dynamic nature of migration behaviour (Woodrey & Chandler, 1997).

A further type of migratory variability describes an intrapopulation *dimorphism* of migration tendency, such that only a proportion of the population migrates and the other remains resident in a single habitat. This is known as partial migration (Lundberg, 1988; Jonsson & Jonsson, 1993; Dingle, 1996), and is evident in many migratory invertebrates,

birds, fish and mammals (Chapman *et al.* 2011). Obligate partial migration, whereby individuals exhibit consistent migration or residence behaviour year on year, is believed to be genetically controlled, whereas facultative, or irruptive, partial migration is recognised as a conditional response, in which individuals may vary their behaviour between years, dependent on external stimuli (Newton, 2010). For example, the incidence and pattern of migration varies between individuals of roe deer and between consecutive years, and is thought to depend on environmental and topographic variability (Cagnacci *et al.* 2011). Obligate and facultative forms of migration may be represented to varying degrees in the same population (Lundberg, 1988). For example, white stork individuals, *Ciconia ciconia*, appear to show a predictable obligate migration of 7,000 km from Europe to East Africa, but in certain years may travel up to a further 4,000 km to southern Africa (Berthold *et al.* 2004). Lundberg (1988) stressed that a combination of fixed, genetic and variable, environmental factors control partial migration and phenotypic variability. Moreover, according to Newton (2010), obligate and facultative migration should be viewed as two extremes on a continuum of migration behaviour, each resulting from adaptations to opposing conditions, such as obligate from predictable versus facultative from unpredictable resource availability. While Newton (2010) intended to focus attention on avian migration, this concept can be readily applied to other migratory taxa, including partially migrant salmonids, the study subject of this thesis.

1.2. MIGRATORY VARIABILITY WITHIN THE SALMONINAE SUBFAMILY

1.2.1. Overview

Salmoninae is a subfamily of the family Salmonidae, comprising seven genera and approximately thirty species of salmon, trout and charr (Nelson, 2006). The species have high economic and social importance, and are distributed throughout the northern hemisphere, and subsequently worldwide following anthropogenic introductions (Nelson, 2006; Jonsson & Jonsson, 2011). All species spawn in freshwater, though some juvenile, sub-adult and adult stages may occur at sea, i.e. are anadromous (Klemetsen *et al.* 2003). The genera *Salmo, Salvelinus* and *Oncorhynchus* are the most studied and represent a remarkable suite of life histories. Three general migration patterns are described: freshwater resident, migratory or partially migratory, with individuals displaying varying degrees of dependence on the marine habitat (Thorpe, 1989). For example, some chinook

salmon, *O. tshawytscha*, may migrate to sea as early as 30 days after fry emergence, providing a stark comparison to stream-dwelling populations of cutthroat trout, *O. clarki*, whose spawning and rearing habitats can overlap in small headwater tributaries (Orlay *et al.* 1999; Beckman *et al.* 2003). Obligate anadromy is demonstrated in certain semelparous species of Pacific salmon, including pink, *O. gorbuscha*, and chum salmon, *O. keta*, whose individuals are highly specialised and must transition between spatially discrete habitats (e.g. upstream freshwater spawning habitat, downstream migration corridors and marine feeding and maturation habitat) during their life cycle (Rieman & Dunham, 2000). In contrast, *Salvelinus* spp. display the least degree of anadromy within the Salmoninae subfamily, but many individuals undergo substantial potamodromous migrations (between distinct freshwater habitats), such as the bull trout, *S. confluentus*, which can typically travel over 100 km within river and lake systems (Hogen & Scarnecchia, 2006). Many salmonid species display partial anadromy, whereby individuals exhibit a degree of flexibility in their use of marine or freshwater habitats for rearing purposes. An excellent example is provided by the rainbow/steelhead trout, *O. mykiss*, whose populations of resident, fluvial, lacustrine and anadromous individuals may co-occur and interbreed, as well as functioning independently (Zimmerman & Reeves, 2000). Typically for iteroparous *Salmo* spp. (Atlantic salmon, *Salmo salar*, and brown/sea trout, *S. trutta*), variation in the age, size and timing at which migration occurs adds further complexity to the array of life histories that can be observed (L'Abée-Lund *et al.* 1989; Metcalfe & Thorpe, 1990).

Riverine environments offer unique opportunities for studying animal migration. For example, rivers are laterally bounded, providing predictable migration routes and enabling direct counts of individuals past fixed monitoring points. Salmonids use a range of aquatic ecosystems, so are ideal organisms for the study of behavioural variation, as well as the biological responses to climate change, habitat degradation and metapopulation dynamics. Like many long-distance migratory species, we may expect anadromous salmonids to be particularly vulnerable to environmental change resulting in habitat fragmentation, loss of heterogeneity and phenological mismatching (Robinson *et al.* 2009). Nowhere is this more disturbing than in the western United States, where river impoundment (enclosure due to anthropogenic structures such as dams and weirs) has led to the extinction of at least 106 obligate migrant Pacific salmon species (Nehlsen *et al.* 1991). The incidence and extent of migration in other salmonid species is versatile and may enhance their resilience in an increasingly unpredictable setting. In fact, for Atlantic salmon and brown trout, climatic induced changes in spawning migration timing have not

appeared to affect breeding success (Dahl *et al.* 2004). Our knowledge of the relative influence of environmental versus genetic variation on the expression of migration tactics is poor, hence challenges arise when predicting the adaptive behaviour of these organisms in order to inform management actions, such as water abstraction and the screening of water intake structures. No rigorous experimental studies have addressed whether variation in migration behaviour arises from local adaptation or phenotypic plasticity, but continued salmonid research could provide valuable lessons about evolution and conservation.

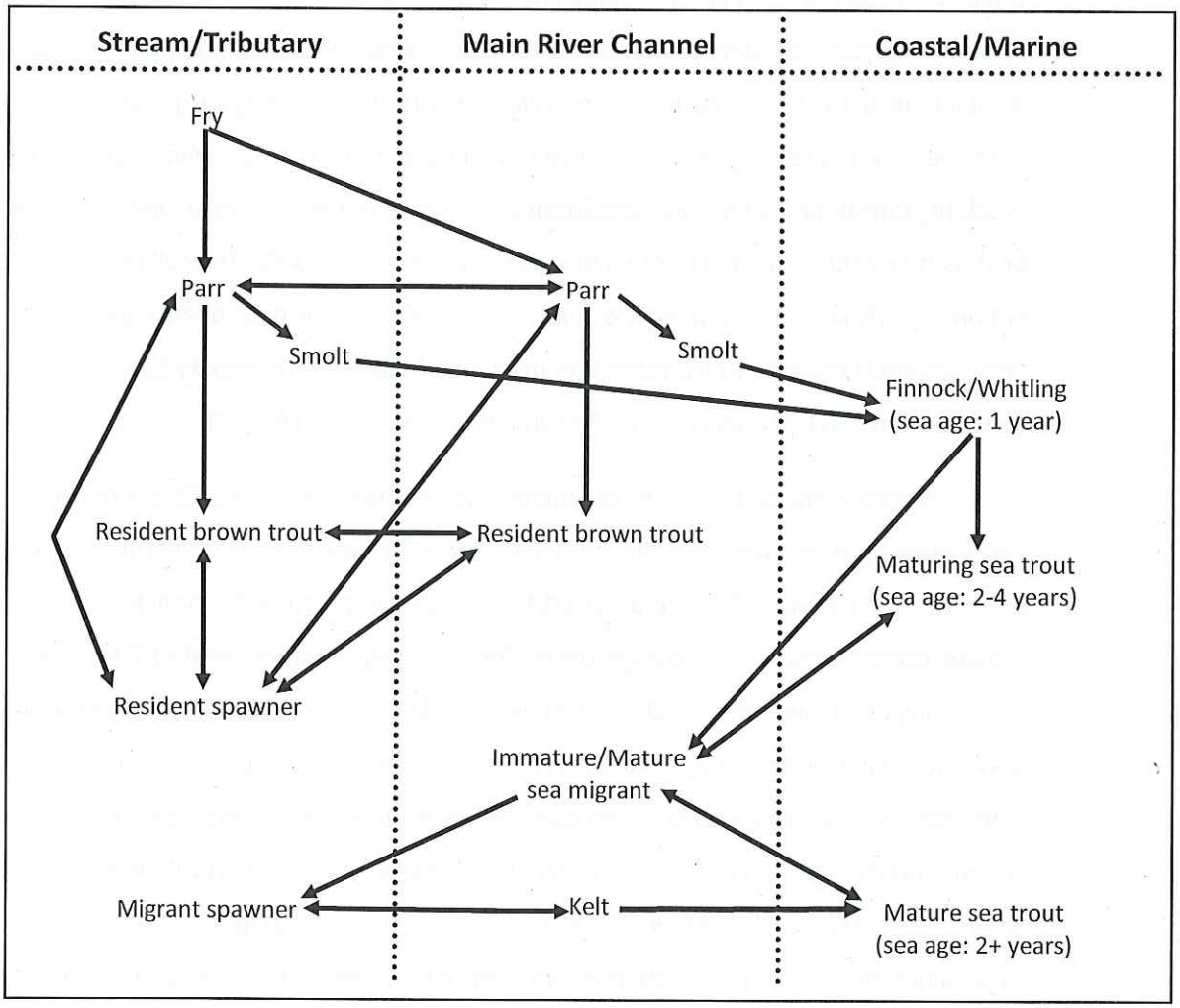

Fig. 1.1: Schematic model of S. trutta life histories, including stream resident, potamodromous and anadromous forms. Adapted from Elliott (1994). Descriptions of the standard terminology are given in Appendix I.

1.2.2. *Salmo trutta*

The brown trout, *Salmo trutta*, is an excellent model organism with which to study plasticity in migration, due to its versatility in juvenile and adult habitat use, the polymorphism of its life history tactics and its wide species distribution throughout Europe, western Asia and northern Africa (excluding anthropogenic introductions) (Elliott, 1994). Spawning occurs in late autumn and early winter, on clean gravel beds in running water, however the behaviour and habitat shifts of individuals between hatching and spawning can be highly variable (Elliott, 1994; Fig. 1.1; Appendix I). A continuum of alternative migratory phenotypes appears to exist in naturally occurring populations, from freshwater stream-resident individuals, through potamodromous migrants, to anadromous sea trout (Cucherousset *et al.* 2005; Jonsson & Jonsson, 2011; Boel *et al.* 2014). In contrast, most Atlantic salmon are anadromous, with few completing their life cycles exclusively in the riverine environment (Thorstad *et al.* 2011). It is this difference in behavioural plasticity that warrants the choice of brown trout as a suitable study species to investigate variable phenology of salmonid migration.

Mature trout may spawn once or, more commonly, a multiple of times, including precocious male parr (Dellefors & Faremo, 1988; Fig. 1.1). As with many other diadromous species, the growth rate, maximum size and reproductive potential of adult migratory trout are enhanced in comparison to sympatric stream-residents (Jonsson, 1985; Klemetsen *et al.* 2003). Hence, their migration can be viewed as a trade-off between the costs of movement to an unfamiliar environment, including energy-demanding physiological changes, and the benefits of improved growth opportunities (Jonsson & Jonsson, 1993; Lucas & Baras, 2001). Interpopulation variation of brown trout migration traits is illustrated in latitudinal clines, as is common for several other salmonid species. For example, the mean smolt age of sea trout is higher in Scottish than Irish and Welsh rivers (Fahy, 1978), and was found to increase from 2.1 years to 5.6 years with a latitudinal increase of 16°N over 102 European rivers (Jonsson & L'Abée-Lund, 1993). This is likely a consequence of decreasing water temperatures and slower growth rates (Klemetsen *et al.* 2003). Populations can also differ in their propensity to migrate. For example, the frequency of freshwater residency is greatest in the south of the species' range, and that of anadromy greatest at the northern range limits (Dodson *et al.* 2013), believed to be due to a greater differential between freshwater and marine productivity at higher latitudes and colder temperatures (Gross, 1987).

Populations of brown trout comprising only one migratory phenotype, i.e. exclusively anadromous, potamodromous or resident, but with open access to the marine environment, are rarely documented in the literature. Nevertheless, Bohlin *et al.* (2001) and Antunes *et al.* (2006) report incidences of entirely freshwater-resident populations at high altitude and low latitudes, respectively. Here, the costs of migration, such as high river gradients, high marine water temperatures and changes to osmoregulatory function, likely outweigh the benefits of migrating to and from a more productive environment (Jonsson & Jonsson, 1993). Even at high altitude, however, Bohlin *et al.* (2001) state that only six of 43 studied river systems contained exclusively stream-resident trout. Complete freshwater residency of spawners in a locality is more commonly recorded in landlocked populations, whose downstream migrants are prevented from returning to spawn either by natural or artificial barriers. Such is the case in Wilfin Beck, in the English Lake District, and the river Laxá, north-east Iceland, where migratory phenotypes are obstructed from reaching spawning sites by waterfalls (Elliott, 1994; Steingrimsson & Gislason, 2002); population connectivity hence occurs in a downstream direction only. It might be expected that exclusively anadromous populations of brown trout would have adaptive significance in highly unproductive or unfavourable stream environments, where the benefits of migration are comparatively high, for example, where low water levels, high water temperature or low oxygen concentration dominate natal stream conditions during summer months. Examples of this are scarce; however in a small Baltic coast stream, subject to recurring drought, it was found that all spawning female trout were anadromous (Titus & Mosegaard, 1992) and aggregations of resident trout were observed at river outlets flowing into the mildly brackish Baltic Sea during dry periods (Østergaard *et al.* 2003).

Examples of differentially and/or partially migrating populations of brown trout are much more numerous. The sex ratio of freshwater, and particularly stream-, residents is highly skewed towards males, and is believed to be the result of intense intrasexual selection for a large body size in females that gives rise to greater fecundity (Jonsson, 1985; Elliott, 1994). For example, Jonsson *et al.* (2001) reported 48.9% of males, but only 3.7% of females adopted the resident phenotype in Norwegian streams. Partial and differential migration are robustly illustrated in data collected by Cucherousset *et al.* (2005) on the Oir River, Normandy, France, where separate individuals were recorded residing in their nursery brooks, as well as travelling to the Oir River, travelling to the larger Sélune River or migrating as far as the sea. The distance of migration appeared to correlate with energetic requirements, inferred by juvenile growth rates in differentially productive environments,

suggesting those with higher metabolic rates migrated further, to the most suitably productive environments. Therefore, fish were monitored growing in a spatial continuum throughout the entire drainage system. Similarly, a continuum of phenotypes exists around Vangsvatnet Lake, Norway, comprising tributary stream dwellers, lake dwellers and anadromous migrants, all spawning together (Jonsson, 1985) and 23 of 43 Swedish river systems studied by Bohlin *et al.* (2001) contained both migratory and stream-resident forms. Partial migration may even extend in a continuum beyond the freshwater phase, for example with respect to the degree of salinity inhabited (Villar-Guerra et al. 2013). This is synonymous with the migration continuum concept (Boel *et al.* 2014), in which the ecological significance of movement is critical in the determination of migration behaviour, irrespective of the distance and environment travelled (Lucas & Baras, 2001). It is this behavioural flexibility that has been advantageous for trout in strongly spatially and temporarily heterogeneous riverine environments, particularly for individuals with high metabolic demands, and will likely be beneficial, in terms of adaptability, during future environmental change.

While detailed accounts of behavioural variability are readily available, fewer studies have explored the proximal mechanisms behind the developmental switch between alternative migratory tactics. It is proposed that all individuals of *S. trutta* have the capacity to adopt any one of the alternative life histories (Dodson *et al.* 2013), since the genetic differentiation between sympatric migrants and residents is low (Hindar *et al.* 1991; Charles *et al.* 2005). Alternatively, the expression of migration behaviour may be greatly influenced by threshold values of liability traits, such as body size (Dodson *et al.* 2013), but using this concept to explain exclusively resident or migratory populations requires the assumption that absent phenotypes must suffer complete mortality, for example due to the metabolic costs of migrating to high altitude (Bohlin *et al.* 2001) or due to drought in the natal stream (Østergaard *et al.* 2003). Some argue outward migration in *S. trutta* is environmentally induced; a conditional response resulting from poor growth opportunities in the natal river section, for example due to high population density (Olsson *et al.* 2006) lack of food (Wysujack *et al.* 2009) or low temperatures (Jonsson & Jonsson, 2009*a*; Morita *et al.* 2014). Ultimately, the future examination and manipulation of hormonal cascades and gene expression will be key to aiding our understanding of the causation mechanisms of variable migration in salmonids, in contrast to the evidence supporting present theories, which is centred on correlational studies.

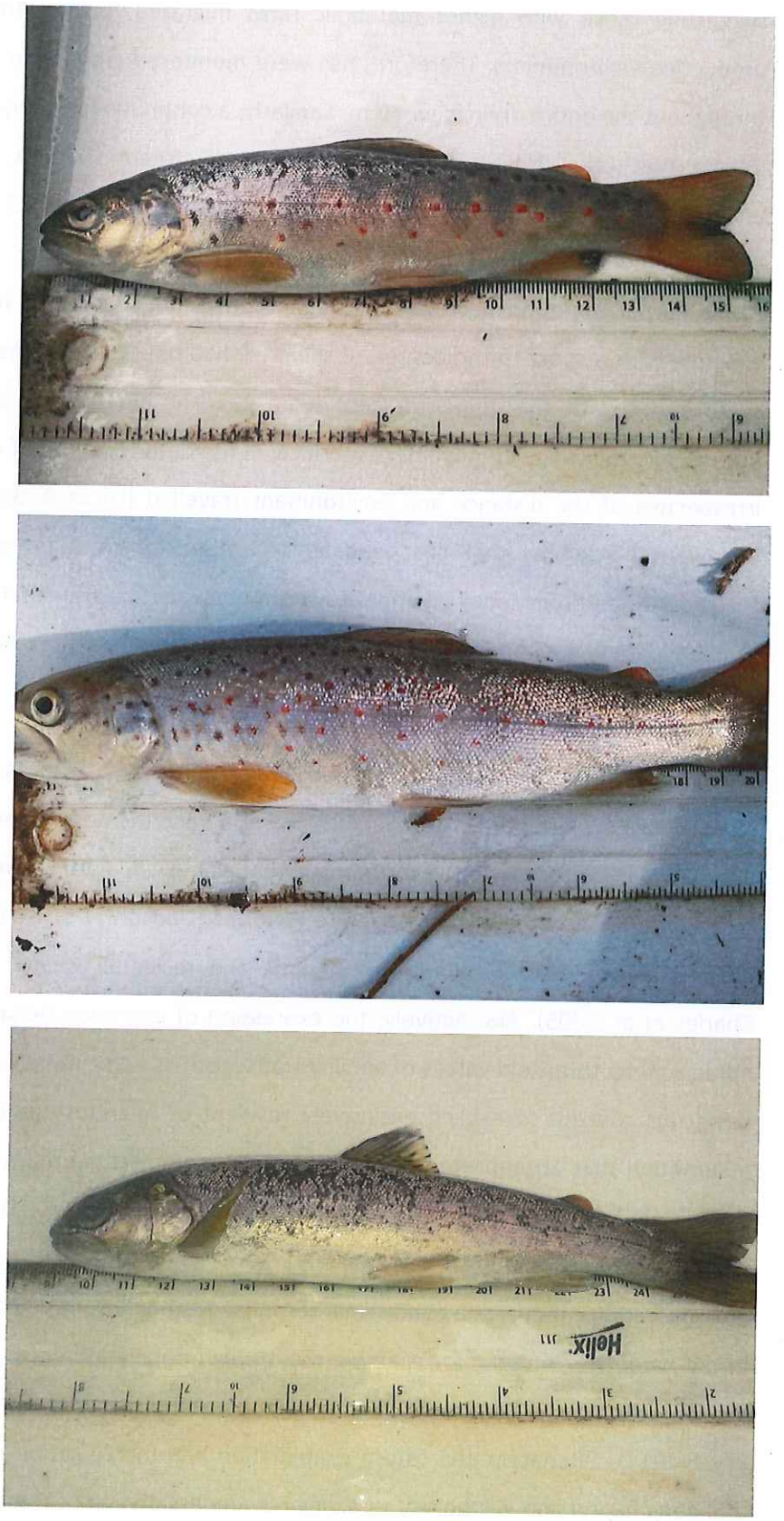

Fig 1.2: S. trutta *parr with clear fingerprint-like vertical bars (parr marks) visible (top), silvered part-smolt with parr marks faded (middle) and silvered smolt with darkened fins and no parr marks (bottom). Fish were caught in the River Deerness, Wear catchment, NE England. Photographs taken on 14/07/14 (by Jeroen Tummers), 23/03/15 and 25/03/15, respectively. See Appendix I for descriptions of standard terminology.*

1.3. PHENOLOGY OF THE SALMONID SMOLT MIGRATION

A substantial amount of research attention concerns the factors regulating downstream migration in wild juvenile salmonids from freshwater to marine environments during spring and early summer, including the exact timing, stimuli and physiological characteristics of individuals (e.g. Jonsson, 1991; reviewed in Klemetsen *et al.* 2003). The phenology of the smolt migration varies temporally between years and geographically between populations, as well as individually within a given year and population. Such a habitat shift is considered a notably hazardous event in the life of a fish, for example mortality of trout in their second year has been estimated at 0.12 % day^{-1} in freshwater, compared to 0.25 % day^{-1} for those at sea (Elliott, 1993). Therefore, migration timing is likely shaped by natural selection. Smolting is regarded as an adaptive specialisation for downstream migration and survival in seawater, but smolt survival ultimately depends on the match-mismatch between physiological readiness and optimal environmental conditions, such as food availability, temperature and predator abundance, in a distinct 'ecological smolt window' that enables successful transition to saltwater (McCormick *et al.* 1998). This distinguishes salmonid smolts from euryhaline species that can move repeatedly (for example, tidally) from freshwater or weakly brackish environments to strongly saline environments and vice versa. An early entry of salmonid smolts into colder seawater may alleviate predator and parasite pressure; however food abundance and salinity tolerance is expected to be reduced (Jensen *et al.* 2012). Behavioural plasticity of migratory timing in the salmonid family thus underpins the ecological success of these species and is the focus of this project.

In general, populations of young salmonids descend to the marine environment over several weeks in spring and early summer, following physiological changes that result in a characteristic silvery body colour, darkened fins, loss/fading of parr marks and a streamlined body shape (McCormick *et al.* 1998; Fig. 1.2). Individuals of a particular year-class may differ in their age at migration, reportedly from one to eight years (Klemetsen *et al.* 2003). It is believed that juveniles must be of an appropriate size-related developmental stage to smoltify in response to environmental cues, therefore age at migration is linked to growth opportunities and, indirectly, to temperature (McCormick *et al.* 1998). Atlantic salmon and brown trout residing at southern latitudes, with longer growing seasons, are known to migrate at a younger age than those further north (Metcalfe & Thorpe, 1990; Jonsson & L'Abée-Lund, 1993), and a decrease in smolt age is predicted with climate warming (Jonsson & Jonsson, 2009*a*). Furthermore, a recent study revealed the proportion

of delayed (older) migrants of masu salmon, *O. masou*, decreased with increasing temperature, but a heterogeneous smolt-age structure may be an important stabilising factor of population dynamics during unfavourable environmental conditions (Morita *et al.* 2014).

Økland *et al.* (1993) found no size threshold for smoltification, although the study incorporated multiple river systems. Instead, those outmigrating from streams to lakes, larger rivers or the sea at a younger age are believed to be the fastest-growing individuals with the highest metabolic rates and energy demands (Økland *et al.* 1993; Forseth *et al.* 1999). Moreover, early migrants shift their niche at a smaller size than their later counterparts (Økland *et al.* 1993; Jensen *et al.* 2012), but food consumption of trout migrants was found to be more than four times higher than residents of the same age, suggesting growth opportunities for early migrants in the natal habitat are constrained (Forseth *et al.* 1999). Evidence also indicates that smolt size and age are positively correlated with nursery stream size, with *S. trutta* smolts as small as 6 cm found in a particularly small stream in southern Norway (Jonsson *et al.* 2001). In such streams with low discharge, larger parr may experience poor feeding and refuge opportunities and early migration may be an adaptation to drought (Klemetsen *et al.* 2003). Nonetheless, the general ability of smolts to survive migration, avoid predation and successfully enter sea water increases with body size (McCormick *et al.* 1998), and hence fast-growing parr may suffer a trade-off between early migration with high mortality risk and extended residency with reduced growth potential.

Some studies have indicated an additional phenological segregation in body size *during* the smolt migration period. Brown trout initially smaller, when tagged, were the latest to migrate in a study in Sweden, such that body length at migration decreased with time during the season (Bohlin *et al.* 1993). These individuals also had higher growth rates than larger subjects, suggesting freshwater growth opportunities had not been constrained. These results are paralleled in a separate report on Atlantic salmon smolt migration in Norway (Jonsson *et al.* 1990). Jensen *et al.* (2012) reported a decrease in smolt size later in the season for Atlantic salmon, brown trout and Arctic charr, *Salvelinus alpinus*, but also an increase in size during the main migration period. It is proposed the earliest migrating individuals had the highest metabolic requirements, due to faster growth rates, while the latest were initially too small to smoltify (Forseth *et al.* 1999; Jensen *et al.* 2012). On the contrary, Hvidsten *et al.* (1995) found no systematic change in length distribution

over the smolting period and one may conclude that individual factors regulating the phenology of smolt migration are likely population-specific.

The physiological and morphological changes that characterise the parr-smolt transformation are predominantly regulated by increasing photoperiod, which ensures the process occurs during spring (Jonsson, 1991; McCormick *et al.* 1998; Björnsson *et al.* 2011). However, since seasonality is a fixed cycle, inter-annual flexibility in the phenology of migration must reflect control from additional proximate releasing factors. A number of other cues have been suggested to influence the commencement of migration behaviour in salmonids, particularly temperature, water discharge, light and lunar cycle (Hembre *et al.* 2001; Hvidsten *et al.* 1995; Jonsson, 1991). Jonsson and Ruud-Hansen (1985) reported that water temperature and rate of water temperature increase alone were responsible for the timing of Atlantic salmon migration from the River Imsa, Norway, with smolts migrating earlier in years with high temperature and/or rapid rates of increase. Similarly, the movements of chinook salmon and steelhead trout in Idaho, USA, have been correlated with increasing stream temperature (Bjornn, 1971). In further support, previous studies have indicated intra-annual latitudinal clines in the timing of smolt migration, with southern populations migrating earlier, but less predictably, than those found farther north (Antonsson & Gudjonsson, 2002; Spence & Hall, 2010). This correlates with geographical variation in seasonal temperatures, such that temperature is thought to influence the rate of physiological processes associated with smoltification, as well as behavioural activity required for migration (McCormick *et al.* 1998). For this reason, some have suggested a threshold temperature for peak migration behaviour around 10°C (e.g. Solomon, 1978; Breau *et al.* 2010). Despite this, Jonsson and Ruud-Hansen (1985) observed smolt migrations at temperatures between 5.8 and 11.2°C. Alternatively, cumulative temperature experience over time may be more influential than absolute values (Zydlewski *et al.* 2005). Ultimately, it is believed smolt survival is maximised by entry into seawater at an optimal temperature that enhances factors such as salinity tolerance and prey availability (Thorstad *et al.* 2012). This is supported by studies that report narrow ranges in sea surface temperature during smolt entry, despite wide ranges in emigration phenology and freshwater temperature across latitudinal gradients (Antonsson & Gudjonsson, 2002).

Recent studies from Scandinavia have found water discharge to be more influential on the timing of downstream migration than temperature for both Atlantic salmon and trout (Aldvén *et al.* 2015; Jensen *et al.* 2012). Furthermore, Hesthagen and Garnås (1986) reported migration behaviour in salmon smolts of the River Orkla, Norway to be triggered

by the first spring peak in water discharge (freshet), despite temperatures between 2-3 °C due to ice-melt. A comparable scenario in Iceland also led to an increase in the number of Atlantic salmon and Arctic charr smolts with increasing water level, but decreasing water temperature (Carlsen *et al.* 2004). Crucially, since individuals must orient themselves in areas of stream channel with the strongest current and activity is most often nocturnal (Jonsson, 1991; Hvidsten *et al.* 1995; McCormick *et al.* 1998), it can be stressed that migration during peak flows remains an active behaviour, rather than passive displacement.

The factors dictating phenology of smolt migration differ in their importance between river systems. This is perhaps due to local adaptations to environmental conditions that result from precise homing of sea migrants to their natal stream, creating reproductively isolated populations (Thorstad *et al.* 2012). For example, in rivers without spring freshets the timing of outmigration is likely linked to temperature-related physiological changes, whereas highly variable water discharge in others may enhance the benefits of migration at high flow, but low temperatures (Jonsson, 1991). Perhaps one would expect longer term studies to reveal greater variability in the importance of environmental drivers of migration, and Hembre *et al.* (2001; 3-year study) and Hvidsten *et al.* (1995; 12-year study) provide evidence for a combined effect of temperature and water flow on migration timing, the relative importance of which fluctuate from year to year with inter-annual environmental variability. Similarly, whilst Jensen *et al.* (2012; 22-year study) report water flow as the most important environmental driver of brown trout migration, a significant relationship between water temperature and daily smolt catch was also evident. Even so, certain populations may be particularly receptive to a single cue, and Jonsson and Ruud-Hansen (1985; 7-year study) found no correlation between any environmental variable tested, other than temperature, and smolt descent.

It has been suggested a hierarchy of environmental cues stimulates smolt migration and may explain the differences in behavioural observations between populations and years (Jonsson, 1991). Common garden and displacement experiments using Atlantic salmon have otherwise revealed individuals exhibit migration patterns related to their natal populations, thus inferring genetic mechanisms of behavioural regulation (McGinnity *et al.* 2007; Stewart *et al.* 2006). Following this, there is some evidence to suggest the timing of migration differs between populations in the same river catchment, with upstream individuals migrating earlier and socially stimulating migration behaviour in those situated further downstream, promoting migratory synchrony (Hvidsten *et al.* 1995; Stewart *et al.*

2006). This may have the adaptive value of reducing the chance of individual capture by predators. Collectively, these findings support the view that cues are largely locally determined by environmental variables that reliably predict favourable oceanic conditions and maximise survival during downstream migration.

In summary, the literature surrounding salmonid life history variation is voluminous (reviewed in Klemetsen *et al.* 2003; Dodson *et al.* 2013), yet elements of juvenile space utilisation and phenology of downstream migration remain unfamiliar and poorly explained. A low number of tracking or trapping studies have targeted juvenile individuals outside the typical spring migration period and estimates of juvenile salmonid population density in rivers are usually carried out in summer when territoriality and site fidelity are regarded as strong (Cunjak, 1992). As such, one is usually unable to distinguish mortality from emigration when examining population losses over autumn and winter. Brown trout are a key element of relatively unaltered cool, oxygen-rich river and lake systems throughout much of Europe. Therefore, understanding the ecology of this species' behavioural variability is important to understanding freshwater ecosystem structure and evolutionary pathways, and becomes vital when we consider its vulnerability to anthropogenic disruptions and population declines (Chapman *et al.* 2011).

1.4. AUTUMN MIGRATION

1.4.1. Atlantic salmon, *S. salar*

It is traditionally considered that juvenile Atlantic salmon remain in their native stream for one to several years before descending the river course as smolts in spring (McCormick *et al.* 1998; Klemetsen *et al.* 2003). Therefore, when considering salmon population dynamics, the freshwater output of a river typically refers to the production of spring migrants (Ibbotson *et al.* 2013). Year-round European and North American trapping studies have, instead, revealed two peaks of emigration in some rivers; a small one comprising parr morphotypes in autumn, and a larger one comprising smolts in spring (Riddell & Leggett, 1981; Youngson *et al.* 1983). This is in contrast to the relatively stable home ranges, in the order of tens of square metres (Steingrimsson & Grant, 2003), adopted by juvenile salmon in summer (McCormick *et al.* 1998). More recently, autumn descents have been recorded in southern British (Pinder *et al.* 2007), Norwegian (Jonsson & Jonsson,

2014) and Baltic populations (Taal *et al.* 2014). Over a six year study, over 40% of salmon parr emigrating from the Brandy Stream to the main River Itchen, southern England, did so during September through to January (Riley, 2007). This is compared to a peak of movement (42%) during April. Furthermore, in the Srahrevagh River, western Ireland, 46%, on average, of native wild juvenile salmon migrants travelled downstream to brackish water in autumn and early winter, with a peak of activity in mid-December (McGinnity *et al.* 2007). Precocious male parr are often abundant amongst autumn migrants (McGinnity *et al.* 2007; Jensen *et al.* 2012), and their early maturation is said to reduce the chance of future smolting (Dellefors & Faremo, 1988). Yet, autumn migration has also been labelled a 'pre-smolt' migration, with the implication that these fish will later smoltify and move to sea (Jonsson & Jonsson, 2011). Jensen *et al.* (2012) also refer to a 'second peak' of juvenile movement in the autumn, despite autumn parr being younger and smaller than smolts of the previous spring. An accurate and consistent use of terminology is required as future research in this field is intensified.

Although Atlantic salmon parr generally adopt limited home ranges, they can be found in a range of habitats from stream riffles, pools and lakes, to estuaries (McCormick *et al.* 1998). Parr inhabiting estuarine environments have previously been assumed to be the remains of an earlier spring smolt run (Power & Shooner, 1996), however recent technological advances have allowed the source of these fish to be examined. For example, passive integrated transponder telemetry has provided a means for remote observations of active movement of juveniles in autumn (e.g. Pinder *et al.* 2007), while the use of otolith strontium to calcium ratios (Sr:Ca) in the Baltic Sea also confirmed that juveniles found in November and December had descended to the brackish environment no more than four weeks prior to capture (Taal *et al.* 2014). The possibility of autumnal smoltification was proposed after observations of 'silver' estuarine parr were made in September (Cunjak *et al.* 1989), however Pinder *et al.* (2007) and Taal *et al.* (2014) found no evidence for smoltification among autumn migrants, which displayed 'strong parr markings'. Similarly, using various methods including a direct translocation from freshwater into full strength sea water, Riley *et al.* (2008) found Atlantic salmon autumn migrants to be physiologically incapable of the osmoregulatory processes required to enter the marine environment. This suggests they reside in brackish tidal waters over winter and only complete the emigration to marine waters in the spring, as smolts with strongly upregulated salt elimination capability. Nevertheless, adjusting the experimental design to limit stress and incorporate a gradual shift in salinity could reveal alternative outcomes.

1.4.2. Brown trout, *S. trutta*

Relatively few accounts of autumnal downstream migrations by trout parr are available, in comparison to the extent of information available regarding analogous behaviour by Atlantic salmon, but given the similarity between these species' phylogenies and life histories, we may expect them to exhibit comparable migratory traits. *S. trutta* parr are often considered to be highly sedentary and territorial before smolting occurs (Klemetsen *et al.* 2003), and a recent study observing autumn migration of Atlantic salmon in northern Norway failed to find parallel behaviour in a sympatric population of brown trout (Jensen *et al.* 2012). Additionally, while Elliott (1994) appreciated that changes in the spatial distribution of juvenile trout do occur in freshwater, it was claimed that most juvenile fish displaced downstream are usually dead or moribund. In fact, Elliott (1986, 1994) did not investigate evidence that small-scale emigration of age 1+ trout parr from Black Brows Beck, NW England, appeared to occur year round and represented a high proportion, relative to spring smolt numbers.

The phenomenon of autumn emigration of trout parr from their natal streams is scarcely recognised as a crucial life history stage in the literature, yet Crisp (1993) reported spring and autumn peaks of juvenile trout movement from a tributary of Cow Green Reservoir, on the River Tees, NE England, suggesting it was dependent on population density. More recently, Jonsson and Jonsson (2009*b*) detected autumn descending trout in the River Imsa, Norway, and labelled them pre-smolts, given the proximity of the trap to the sea water limit. While autumn migrants showed higher growth rates in the subsequent growth season than spring migrants, they exhibited the highest marine mortality, estimated by the proportion of fish returning to the river to spawn, possibly indicating a trade-off between the two life strategies (Jonsson & Jonsson, 2009*b*). An autumn descent of anadromous trout parr has also been documented in the Baltic Sea, with five juveniles caught in Eru Bay in the months of November and December (Taal *et al.* 2014), though it should be noted that the Baltic is weakly brackish and does not require marine-level osmoregulatory competency for survival. Wild trout census data collected in the Burrishoole catchment, western Ireland, also clearly show an 'autumn' downstream movement of juveniles, which peaks in December (Marine Institute, 2014), and Holmes *et al.* (2014) concluded juvenile emigration from the Rainy River, New Zealand, followed a two-phase pattern, with early emigration of larger individuals in autumn during peak flows prior to spring smolting. The netting methods employed by Taal *et al.* 2014 were restricted to monthly sampling events within a small area of Eru Bay, 2km from the River Loobu's

outlet, and hence the results likely understate the river's true population of juvenile autumn migrants. By contrast, daily trap counts or continuous monitoring methods, such as those employed by the Marine Institute (2014) and Holmes *et al.* (2014) are much more representative of fish behaviour at the population level. These examples represent only a handful of river systems, and it will be crucial to determine whether similar migratory phenotypes are present elsewhere, in order to account for their behaviour in population models and management programmes.

1.4.3. Ecological significance

A number of questions regarding the ecological significance of autumn migrations of salmonid juveniles remain. Potential mechanisms could involve intrinsic factors, such as fish size, energy status and position in a dominance hierarchy, or extrinsic factors, such as population density and habitat quality (Armstrong & Griffiths, 2001; Bjornn, 1971; Huntingford *et al.* 1992). Emigration of precociously mature male Atlantic salmon parr from the Girnock Burn, Scotland has been shown to follow the influx of mature adult salmon during the spawning season (Buck & Youngson, 1982). Similarly, in the River Halselva, Norway, 89% of juveniles emigrating in autumn were males, 92% of which were mature (Jensen *et al.* 2012), and a sample of autumn migrating salmon parr from Wings Brook, Newfoundland, contained only ripe or spent males (Hutchings, 1986). This phenomenon may result from a re-establishment of dominance hierarchies during spawning, or may have a reproductive motivation, to maximise sexual contact between precociously mature males and adults (Buck & Youngson, 1982; McGinnity *et al.* 2007). Yet, a significant remaining proportion of the autumn migrating population are either females or sexually immature males (McGinnity *et al.* 2007; Huntingford *et al.* 1992), and likely depend on different seasonal and biological cues to initiate movement (Buck & Youngson, 1982).

Autumnal peaks of movement have also been associated with elevated stream discharge (Youngson *et al.* 1983; Holmes *et al.* 2014), or poor overwintering habitat, such as a gravel substrate too small to provide refuge (Riddell and Leggett, 1981). Alternatively, movements may reflect a fall in nursery stream carrying capacity or the need for greater dietary energy input. Evidence for this resides with riverine parr overwintering in lacustrine habitats, which have been shown to exhibit enhanced growth and survival rates (Hutchings, 1986). Some have shown autumn migrants are predominantly larger parr with faster rates of growth (Huntingford *et al.* 1992; McCormick *et al.* 1998; Holmes *et al.* 2014), however

Ibbotson *et al.* (2013) found no difference in size or condition factor between autumn and spring migrants at the time of tagging (in September). Neither was there any effect of density on the production of autumn migrants. The probability of age-0 parr becoming autumn migrants did, however, increase with proximity to the tidal reaches, which is in keeping with an autumnal re-distribution of parr in a downstream direction, rather than a targeted marine migration (Ibbotson *et al.* 2013), or alternatively reflects greater mortality with increased migration distance. It is unclear whether autumn and spring migrants differ in their genetic origin (Ibbotson *et al.* 2013); however McGinnity *et al.* (2007) demonstrated the proportion of autumn migrating fish was always greater in wild native, than farmed, populations, suggesting genetic variation is an important additional determinant of phenotypic characteristics.

To conclude, it may be reasonable to suggest that autumn and spring migrants represent alternative evolutionarily stable strategies, whereby an extended period of migration has the adaptive advantage of spreading the risks of mortality during shifts between unpredictable environments (McGinnity *et al.* 2007). Due to the limitations of tracking over large spatial scales, no studies have explored the marine movements of autumn migrants, yet with improved tracking technology (smaller tracking devices, more automation, less expense etc.), it is the hope that their behaviour at sea will be determined. Given the altitudinal and latitudinal gradients in migratory tendency observed for many salmonids (Dodson *et al.* 2013), it would be interesting to explore the effect of geographic location on incidence of juvenile autumn migration. An in-depth evaluation of the temporal variability of the extent of autumn migration, including trout, is also needed, along with further studies concerning the sex ratio, genetics, survival and fitness consequences of autumn migrant individuals.

1.5. SUMMARY AND RESEARCH DIRECTION

This chapter has reflected upon the variability of migration within the animal kingdom and, more specifically, within the salmonid fishes, highlighting a wealth of knowledge regarding certain aspects of behaviour, but also areas of ambiguity needing further investigation. While the juvenile salmonid smolt migration has been well-studied, there is a growing body of evidence supporting alternative migratory phenotypes that may exist within the theoretical migration continuum concept (Cucherousset *et al.* 2005; Dodson *et al.* 2013; Boel *et al.* 2014). With particular reference to the timing of

downstream migration, a number of environmental regulators and phenotypic determinants have been proposed (e.g. Ibbotson *et al.* 2013; Holmes *et al.* 2014), however challenges remain in understanding the evolutionary mechanisms responsible for behavioural variation.

Despite enhanced awareness of an autumn downstream migration phenotype in juveniles over recent years, it remains uncertain whether autumn migrants are destined to become anadromous or potamodromous adults, or whether they are displaced residents, for example by strong flows, competition or a combination of these. The value of alternative wintering habitats, in terms of survival, smolt output, performance in the sea and ultimately fecundity, is important for river and fisheries managers in directing conservation, regulation and habitat management (Ibbotson *et al.* 2013). Jensen *et al.* (2012) predict survival of autumn emigrants from the River Halselva to be low, due to low discharge during winter caused by ice cover and the lack of an estuary in which individuals could take refuge. In other studies, autumn Atlantic salmon emigrants have been detected returning as sea run adults, indicating their viability, and hence stock-monitoring programmes that do not account for such behaviour risk underestimating smolt output and subsequent recruitment (Riley *et al.* 2009; Youngson *et al.* 1994). Further investigation is necessary to understand the motivation for an alternative migratory phenotype in salmoind parr, particularly for trout; is it environmentally induced, genetic or a strategic trade-off between the benefits and costs of early arrival in a marine environment?

This study set out to record the precise timing and extent of juvenile *S. trutta* migration from natal stream habitats over an eight month period, and to provide new information on the drivers of autumn migration, in parallel to the wealth of literature concerning spring smolt migration. This will be central in determining the ecological requirements of parr prior to marine life, and facilitating more informed stock management (Riley *et al.* 2009). Ultimately, a thorough understanding of behavioural variation in this species will be crucial in predicting its responses to degrading or unstable future environments. Therefore, the specific aims of this research were: -

1) To determine and compare the phenology of migration from two European streams, the River Deerness (north-east England) and River Villestrup (Jutland, Denmark), using Passive Integrated Transponder (PIT) telemetry. Migration was expected to be influenced by the streams' ecological characteristics, with a greater incidence of

migration predicted with increased proximity to the marine environment, due to reduced migration costs.

2) To evaluate the effects of environmental, subject-specific and tag site-specific variables on the timing of migration in both locations, in order to offer explanations to the ecological significance of behavioural phenotypes. Incidence of migration was predicted to increase with elevated temperature and river discharge, with increased fish size and condition and at higher trout densities.

3) To investigate changes in demography and site fidelity over summer, autumn and winter in the Deerness using mark-recapture surveys, with the view to provide additional information on rates of survival and local dispersal. Survival and site fidelity were predicted to be high during summer.

Chapter 2: Methodology

2.1. RATIONALE

The methodology of this study encompassed both conventional and technologically advanced approaches to investigate the demography and movement of wild populations of brown trout. Understanding population dynamics and the extent of site fidelity, dispersal and migration throughout the year, and with respect to habitat and environmental variables, required a combination of repeat samples, continuous environmental monitoring, mark-recapture surveys and biotelemetry. Mark-recapture surveys have long been used to assess population size, recruitment, survival, site fidelity and the probability of capture (e.g. Jolly, 1965; Seber, 1965), but recent developments permit a wide variety of marking techniques, such as PIT tags, radio tags and acoustic tags. PIT tags are biocompatible, glass cylinders encasing an electronic microchip (Lucas & Baras, 2000). When energised by an interrogator, their function is to automatically transmit a signal detailing their unique alphanumeric code, which is used for identification of individuals. PIT telemetry has become a successful, cost-effective means of remotely monitoring fish movements, particularly due to the small size of tags, which reduces adverse effects on survival, growth and swimming performance (Cooke *et al.* 2013; Larsen et al. 2013). The longevity and unique coding of individual PIT tags is advantageous for both spatio-distribution and long-term migration studies in a range of fish species (Lucas & Baras, 2000; Aarestrup et al. 2003; Svendsen et al. 2007), and, while large-scale tracking studies can be limited by tag detection ranges, the continuous monitoring of fish movement in small streams is made possible with fixed antennae (Castro-Santos et al. 1996). PIT telemetry has greatly improved our understanding of fish behaviour (Cooke *et al.* 2013), and was ideally suited for use in the present study.

A significant limitation of many migration studies is that they concern only a single population of organisms, meaning conclusions are drawn from a single experimental replicate. An advantage of the present study was the use of two study streams with similar oceanic climate, latitude (~55° N), elevation and stream size to reflect independent replicates. This was useful in determining whether juvenile autumn/winter migration was more widespread than previously assumed, and enabled a direct comparison of trout behavioural characteristics between sites. The River Deerness is a tributary of a larger

freshwater river system, while the River Villestrup flows directly into a brackish fjord, therefore ecological characteristics differ somewhat by study site, most notably the rivers' proximity to the marine environment. This led to the establishment of the hypothesis that migration tendency would increase with distance downstream.

The methods of data collection presented in the following chapter represent the combined efforts of a number of researchers, namely Jeroen Tummers (Durham University) and members of the Technical University of Denmark (DTU), alongside the author. Due reference to their specific contributions are given in parentheses in the text. Following data collection, all data analyses were solely conducted by, and are the original work of, the author.

2.2. STUDY AREAS

2.2.1. River Deerness

The River Deerness is a first to fourth stream-order tributary of the River Browney (typical stream width in study reaches: 3-10 m), situated west of Durham City in north-east England (54°44' N, 1°48' W) and flows west to east, ultimately into the North Sea via the River Wear (Fig. 2.1). The Wear has large stocks of Atlantic salmon and sea trout with resistivity (partial) counts of upstream migrants at Durham, 29 km from the sea, averaging 15,593 fish per year between 2007 and 2014 (Environment Agency, 2015; resistivity counters detect the passage of a fish by sensing a change in the electrical resistance of the water). The annual mean discharge of the Browney is 1.6 m^3s^{-1}, 3.7 km downstream of the Deerness confluence (NRFA, 2015). That of the Deerness is estimated at 0.5 m^3s^{-1}, based on its approximate contribution to the flow of the Browney. Wild populations of trout, grayling (*Thymallus thymallus*), minnow (*Phoxinus phoxinus*), bullhead (*Cottus gobio*), stone loach (*Barbatula barbatula*), and eel (*Anguilla anguilla*) are present in the stream. The brown trout population consists of multiple cohorts, with a mixture of resident and migratory adults, including anadromous sea trout (E. Winter, J. Tummers unpublished data).

The Deerness drains a catchment of 52.4 km^2 and is 16.3 km long, consisting largely of grassland to the west, and transitioning to broadleaf woodland and lower-lying arable areas in the east. Six Deerness study sites were dispersed over *ca.* 15 km of stream length (T1-T6; Fig. 2.1). The chosen sites were locations of eight low-head engineered river structures (T1: road bridge apron; T2: weir and pipe bridge; T3: two pipe bridges; T4: pipe

bridge; T5: culvert; T6: pipe bridge), of which six had been removed or modified with passage easements. They were not expected to be significant obstacles to downstream migration. The quality of habitat for juvenile trout was assessed at each of the sites using walk-over surveys at base flow conditions on 3 June 2014 (conducted by J. Tummers), based on the protocols outlined by the Scottish Fisheries Coordination Centre (SFCC). In-stream and riparian habitats were characterised based on bank width, water depth, substrate, flow and fish cover (SFCC, 2007) over 80 m stream sections upstream and downstream of each structure (160 m total). Where two structures were located close to one another, i.e. within 160 m of each other (sites T2 and T3), surveyed distances between the structures were reduced. Details of habitat categorisations and abbreviations are given in Table 2.1.

2.2.2. River Villestrup

The River Villestrup (56°46' N, 9°55' E) is the primary freshwater source for the strongly brackish Mariager Fjord, ultimately exchanging with the Kattegat Sea on the east coast of Jutland, Denmark (Fig. 2.1). The river flows north to south, with a mean annual discharge of 1.1 m^3s^{-1} (Villar-Guerra *et al.* 2014). It is approximately 20 km long, has a typical stream width in the studied reach of 4-10 m and drains a catchment of 126 km^2. The Villestrup represents the most important sea trout tributary to the Mariager Fjord, with the average density of wild young of the year trout estimated at 125 per 100 m^2 (HELCOM, 2011). No stocking occurs. Populations of eel, stickleback (*Gasterosteus aculeatus*), river lamprey (*Lampetra fluviatilis*), brook lamprey (*L. planeri*) and brook trout (*Salvelinus fontinalis*) are also present in the system. The inner fjord has salinities of 12-17 PSU in the upper 10 m of the water column used by trout, while deeper areas are more saline but often hypoxic. The shallow outer fjord has salinities of 20-25 PSU. The Villestrup joins near the junction between the inner and outer fjord areas, on the north shore (Fig. 2.1).

2.1: Substrate and flow classification definitions and abbreviations for river habitat surveys according to the Scottish Fisheries Coordination Centre (SFCC, 2007).

Variable	Code	Definition
Substrate	HO	**High Organic**: Very fine organic matter
	SI	**Silt**: Fine, sticky, mostly inorganic material, individual particles invisible
	SA	**Sand**: Fine, inorganic particles, < 2mm diameter, individual particles visible
	GR	**Gravel**: Inorganic particles 2-16mm diameter
	PE	**Pebble**: Inorganic particles 16-64mm diameter
	CO	**Cobble**: Inorganic particles 64-256mm diameter
	BO	**Boulder**: Inorganic particles >256mm diameter
	BE	**Bedrock**: Continuous rock surface
Flow	SM	**Still Marginal**: < 10cm deep, water still or eddying, no waves form behind a 2-3 cm wide rule placed in the current, smooth surface appearance, water flow is silent
	PO	**Pool**: water flow slow, eddying, no waves form behind a 2-3 cm wide rule placed in the current, smooth surface appearance, water flow is silent
	GL	**Glide**: water flow moderate/fast, waves form behind a 2-3 cm wide rule placed in the current, smooth surface appearance, water flow is silent
	RU	**Run**: water flow fast, unbroken standing waves at surface; water flow is silent
	RI	**Riffle**: water flow fast, broken standing waves at surface; water flow is audible

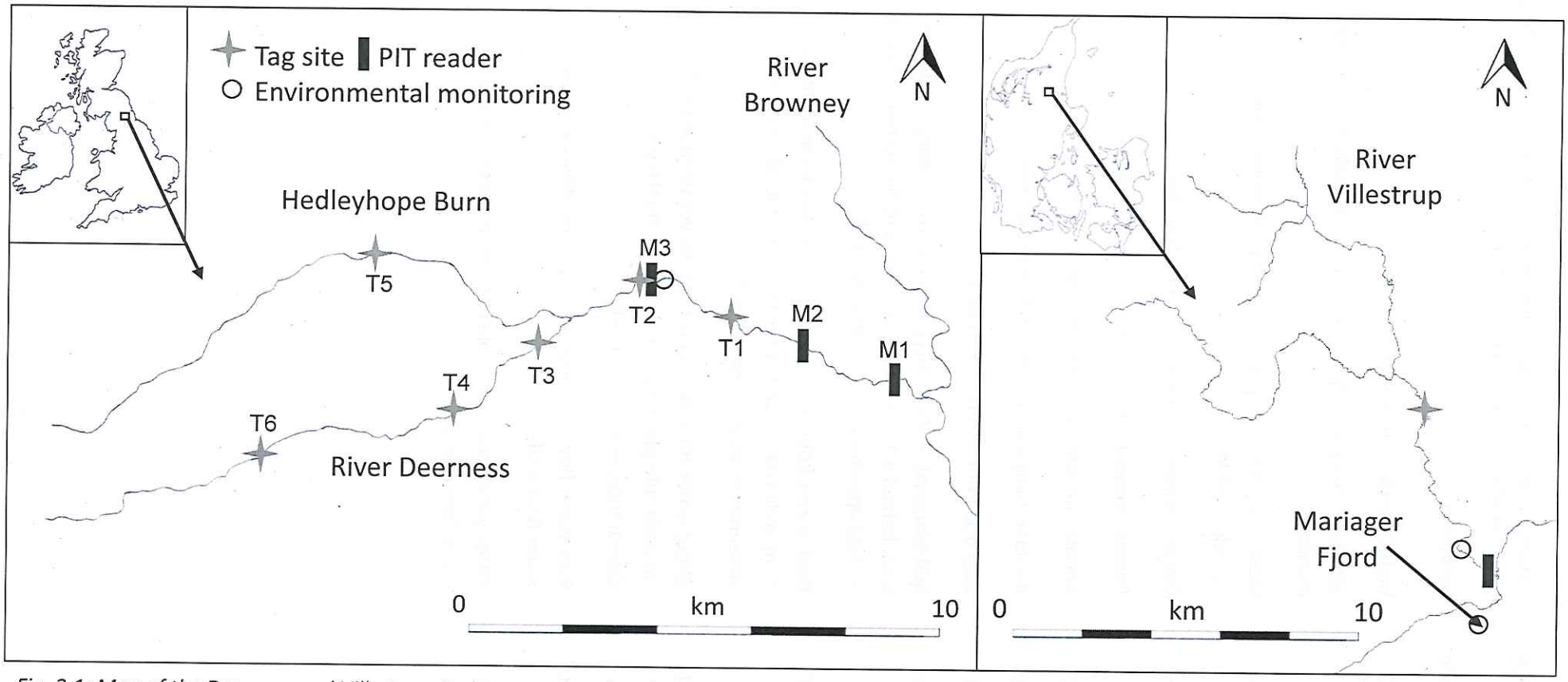

Fig. 2.1: Map of the Deerness and Villestrup study areas, showing the locations of PIT tagging sites, fixed PIT readers and environmental monitoring stations with stars, thick lines and open circles, respectively. Inset maps show the location of the study areas nationally.

2.3. FISH SAMPLING AND PIT TAGGING

Trout in the Deerness system were captured for PIT-tagging using electric-fishing equipment (pulsed DC Electracatch WFC4, Wolverhampton, UK and 1 KVA Honda generator) at each study site (conducted by J. Tummers, with assistance from the author from 20 August 2014). Tagging was conducted on 19 occasions between 9 July and 12 September 2014 (n = 643), up to 140 m directly upstream and downstream of each barrier. A small number of individuals (n = 23) were also tagged on 6 November 2014 at T6 (mean FL ± SD of all trout = 151 mm ± 23). In the Villestrup, trout were captured for PIT tagging on 26 September 2014 (n = 490; mean FL ± SD = 147 mm ± 27), using electric-fishing equipment at a single location *ca.* 8.5 km upstream of the river outlet (Fig. 2.1; conducted by DTU). Sampling was always carried out when conditions were good i.e. stable weather conditions and low water flow. After visually inspecting individuals for injuries, unharmed fish from each study area were anaesthetised (Deerness: buffered MS-222, 100 mg L^{-1}; Villestrup: Benzocaine, 25 mg L^{-1}) until operculum rate was slow and irregular, weighed (to 0.1 g), measured (FL to 1 mm), sampled for scales and surgically implanted with a PIT-tag (Texas Instruments; model RI-TRP-RRHP, HDX, 134.2 kHz, 23.1 × 3.85 mm, mass 0.6 g in air [for fish ≥120 mm (Larsen *et al.* 2013) and ≤250 mm FL] or 12.0 × 2.12 mm, mass 0.1 g in air [for fish <120 mm FL; Deerness only, n = 7]). PIT tags were inserted into the peritoneal cavity through a small incision on the ventral surface, posterior to the pelvic girdle. Tags and instruments were disinfected with 90% ethanol and air dried before use. All procedures were carried out by an experienced fish surgeon and under U.K. Home Office Licence or with permission from the Danish Experimental Animal Committee. Following recovery, all individuals were returned to their site of capture.

2.4. MEASURES OF DEMOGRAPHY

Quantitative estimates of trout densities (n·100 m^{-2}) were made at each of the Deerness tagging sites, using a multiple-pass depletion method (Carle & Strub, 1978), both in late June/early July 2014 (by J. Tummers in conjunction with tagging events) and late March 2015, immediately prior to the main smolt run. This was implemented in R 3.1.1 (R Core Team, 2014) with use of the FSA package (Ogle, 2012), and was also used to estimate capture efficiency of single-pass and triple-pass fishing episodes. Densities of specific age groups were estimated based on the results of the length-frequency decomposition assessment (see below).

The collection of scale samples from each tagged trout was intended to facilitate age determination, through the analysis of growth rings and annuli. Unfortunately, difficulties in interpreting freshwater growth patterns due to numerous eroded and/or repaired scales meant annuli were unclear and this was not possible. Alternatively, length-frequency distributions, collected from multiple-pass depletion surveys in June-July 2014 and March 2015, enabled age structure interpretation using Bhattacharya's decomposition assessment in the FiSAT computer programme (Bhattacharya, 1967; FAO-ICLARM Stock Assessment Tools). This involved the separation of length-frequency distributions into their component normal distributions or pseudo-cohorts, by identifying the presence of modes (King, 1998). For each mode, the mean fish length and standard error were determined. Separation indices (I_S) greater than 2.0 indicated significant difference from other modes (Bhattacharya, 1967). For simplicity, all fish comprising the smallest mode of each survey (age 0+ in 2014; see Appendix I) were termed young-of-the-year (YOY), and all those comprising the second and subsequent modes of each survey (age 1+ and older in 2014) were termed parr. Tagged individuals recaptured in March 2015 were removed from this analysis.

The sex of migrating individuals was of interest due to the skewed sex ratio of phenotypes observed in partially migrant populations of salmonids (e.g. Jonsson, 1985). Cheap molecular methods enabling the sexing of juvenile trout from tissues samples were not available at the onset of this study, but electrofishing surveys were carried out in November 2014 to determine the proportion of the juvenile population that were precociously mature males. This was employed at sites T1 to T5 and was achieved by gently rubbing the flanks of each individual. Those producing milt from the vent on the underside of the body were termed spermiating and hence, reproductively mature.

2.5. REPEAT RECAPTURE SURVEYS AND CJS MODELLING

Following the initial capture and PIT-tagging of trout at sites along the Deerness, multiple recapture sessions during the summer of 2014 (performed by J. Tummers) enabled an examination of site fidelity and probability of survival. Over a period of *ca.* two months, three single-pass electrofishing surveys were conducted at each site. The distance surveyed consisted of contiguous stop-netted 20 m stream sections, and was increased in each session from initially 100 m to finally 200 m upstream and downstream of each structure. Where two stream structures were located close to one another (sites T2 and T3)

surveyed distances between the structures were reduced. During the first recapture session at sites T2, T3 and T4, and during the first two recapture sessions at sites T1, T5 and T6, any untagged individuals captured were tagged and subsequently released back into the population. During the remaining surveys, untagged individuals were released without individual identification. The frequencies of maximum longitudinal distances covered by each recaptured fish from a previous site of release showed a typical inverse-power distribution. Following the methods of Bubb *et al.* (2004), linear transformation using a double-ln plot enabled regression analysis. Upstream and downstream dispersal were analysed separately and the regression lines compared. To maximise sample size, the recorded dispersal ranges were combined from all study sites.

The initial PIT-tagging of trout at each site along the Deerness was performed in 60 m stream sections upstream and downstream of each barrier. Only these stream sections remained common to all surveys, hence for analysis of survival probability, only the fate of individuals tagged and recaptured in these sections was represented in a capture history (Lebreton *et al.* 1992). Analyses using standard Cormack-Jolly-Seber (CJS) live-recapture models were run in MARK 8.0 (White & Burnham, 1999) using capture history matrices, where one time interval equated to one month, or 30 days. Maximum likelihood estimates of apparent survival, ϕ, were computed, where ϕ represents the probability that an individual survived from capture occasion i to $i + 1$ and was available for recapture at capture occasion $i + 1$. This approach does not assume a closed population, without immigration and emigration, however permanent emigrants inevitably appeared to have died (White & Burnham, 1999). Global starting models with time-variant survival and recapture probabilities were tested for goodness-of-fit (GOF). Lack of fit was indicated by a significant GOF test. An estimated level of overdispersion, C-hat, was calculated by dividing the χ^2 value by the d.f. (Burnham & Anderson, 2002). Separate CJS models for each study site were then run with either time-variant or time-constant survival probability, while recapture probability was constrained to a fixed site-specific value, estimated for parr in the summer of 2014 using the results of the multiple-pass depletion fishing. Model selection (time-variant or time-constant survival probability) followed the minimisation of corrected Akaike's information criterion (AIC_c) values, which represents the best compromise between lack of precision (too many parameters) and bias (too few parameters) (Burnham & Anderson, 2002). Where no significant difference was found between two models, selection favoured the more parsimonious one (with the fewest

parameters). Normalised Akaike weights represented the relative probability of a model and were also used for interpretation.

Recapture surveys were additionally conducted in March 2015, alongside the depletion fishing surveys, and in July 2015 (by J. Tummers) to examine longer-term site fidelity and growth rates since previous capture events. Growth rate (%day^{-1}) is commonly estimated using the parameter fish mass (Elliott & Hurley, 1995), since it is a more sensitive descriptor than fish length, given the standard length (L)-mass (M) relationship:

$$M = aL^3$$

where a is a measure of fish condition. Measurements of mass were not available for the July 2015 sample. Instead fish length was used to compare growth rates between capture events and to facilitate comparison with the Bhattacharya length-frequency decomposition assessment. Linear regressions were performed to investigate the value of fish mass and length at the time of tagging in predicting rate of growth to recapture events in March 2015 and July 2015. An analysis of standard residuals identified one outlier, measuring 241 mm, which was removed from the data set. For individuals recaptured in both surveys, growth rates were compared between seasons using a paired-samples t-test. In March, the developmental states of tagged trout (parr, smolt [including part-smolt] or adult) were also recorded based on phenotypic characteristics (e.g. parr marks, body colour, body shape; Fig. 1.2; Appendix I), in order to predict the seaward movement of certain individuals.

2.6. PIT TELEMETRY

Three pairs of stream-width swim-through half-duplex (HDX) PIT antennae were installed on a 5 km stretch of the lower Deerness (Fig. 2.1-2.4; Bolland *et al.* 2009), operational from 24 September 2014 at stations M2 and M3 and 13 October at station M1, until 31 May 2015. The use of multiple monitoring stations facilitated calculations of the speed of migration for trout in the Deerness. Due to occasional battery failure and a damaging high flow event in November causing severe loss of efficiency, the stations M1, M2 and M3 were operational 95.6, 98.1 and 98.1 % of the time, respectively. On the Villestrup, a single pair of mains-powered antennae were placed 300 m upstream of the river outlet (Fig. 1), functional 88.7 % of the time from 26 September 2014 to 31 May 2015 (operated by DTU). Tags were detected by time-synchronised Master and Slave HDX readers (Texas Instruments SX2000; in-house build), interrogating the pairs of antennae

eight times per second (Castro-Santos *et al.* 1996). Upon detection, a tag's code, along with date, time and antenna number, were either automatically downloaded or stored on a flash memory card, from which data was regularly downloaded onto a portable laptop. Detection ranges between 20 and 80 cm were achieved and correct function on the Deerness was confirmed by passing a test tag through each antenna before and after each battery change (every 4 ± 2 days), and by more detailed range testing periodically. Each Villestrup antenna had a timed auto-emitter check tag (Oregon RFID). Detected individuals were categorised based on their direction of movement, upstream or downstream and any Deerness fish tagged within 260m of M3 and detected at M3 only were labelled residents. For the purpose of this study, and by reference to standard terminology applied elsewhere (e.g. Ibbotson *et al.* 2013), all fish detected prior to 1 February were labelled autumn migrants, while those detected from 1 February to 31 May were labelled spring smolts. Detection frequencies were extracted using a 24 hr interval filter between repeat detections, per individual, per site. Additionally on the Villestrup, a Wolf-type trap (Wolf, 1951) situated directly downstream of the PIT antennae captured migrating smolts from 18 March 2015 until the end of the study (operated by DTU).

Figure 2.2: Weather-proof box housing Deerness PIT logging equipment and batteries. Photograph taken on 24/09/2014.

Figure 2.3: Pair of PIT antennae shown with support structures. Tuning boxes were housed in black plastic for protection. Photograph taken on 24/09/2014.

Figure 2.4: Bank-to-bank view of PIT antenna. Photograph taken on 24/09/2014.

On the Deerness, antennae were constructed bank to bank and covered the complete stream cross-sectional area in all but the very highest water flow conditions (< 1% of study period). Swim-through detection fields were routinely checked for blind spots. Theoretical antenna efficiencies of 99, 100 and 100% were achieved for Deerness stations M1-3, respectively, by routinely passing a test tag through the system. In practice, several factors influence a tag's probability of detection, including environmental conditions, tag velocity, tag orientation and the presence of other tags (Zydlewski *et al.* 2006; Burnett *et al.* 2013). A practical estimate of efficiency is, hence, given by the ratio of fish detected at a site that are known to have passed through (Zydlewski *et al.* 2006). For the upstream antenna at M1 (M1:2) this was estimated at 88.1%, for antennae at M2 (M2:1 and M2:2), at 96.1% and 94.2%, and for the downstream antenna at M3 (M3:1), at 49.0%. The detection efficiency of the downstream antenna at M1 could not be estimated using this method, due to the absence of detection equipment downstream. Likewise for the upstream antenna at M3, estimates were prevented by the time lag between tagging events and the onset of monitoring, meaning the location of individuals prior to detection was uncertain. While the estimated efficiency for M3:1 was much lower than is appropriate for telemetry studies, multiple antennae created redundancy in the system, and the probability of detection at one or more of M1:2, M2:1, M2:2 and M3:1 was estimated at >99 %, assuming independent probabilities of detection at each of the antennae. Using Zydlewski *et al.*'s (2006) method, the efficiency of the Villestrup station was estimated as 86.5% in spring, by identifying the proportion of tagged individuals caught in the downstream trap that were also detected by the PIT antennae. Since the trap had an impounding effect and raised water levels, antennae efficiency previous to trap operation was likely higher, but was not quantified.

2.7. ENVIRONMENTAL MONITORING

One logger (HOBO®; model U20-001-01; Onset Computer Corporation), situated at M3 on the Deerness (Fig. 2.1), recorded water temperature (accuracy ±0.4 °C) and water pressure (accuracy ±0.6 kPa) at 15-minute intervals and was operational throughout the study period. Using HOBOware Pro software, the Barometric Compensation Assistant enabled the calculation of water level (±0.5 cm), upon input of hourly barometric pressure records, obtained from the Met Office Library for a location (of similar altitude) 30 km from the study site. On the Villestrup, temperature was measured at the upper antenna (Tinytag plus 2; model TGP-4017, www.gemenidataloggers.com) and water level records were

obtained from a fixed gauging station ca. 1 km upstream of the river outlet (Fig. 2.1; data obtained by DTU).

2.8. STATISTICAL ANALYSES OF PIT TELEMETRY

The influence of environmental factors on the timing of downstream movement was analysed using generalised linear models (GLMs), comparing daily detection frequency of first detections (N_i) on day i with fluctuations in average daily water temperature (°C; $Temp_i$), photoperiod (PP_i), average daily water level (m; WL_i) and the change in average daily water level (m; ΔWL_i). Initial Poisson GLMs revealed non-linear residual patterns and overdispersion, which was corrected for using the negative binomial distribution with a log-link function. The model is specified in the following equations, where μ = mean, k = dispersion parameter, $E(N_i)$ = expected number of detections on day i, var = variance, F = linear predictor function, α = common intercept and X = an independent factor:

$$N_i \sim NB(\mu_i, k)$$

$$E(N_i) = \mu_i$$

$$var(N_i) = \mu_i + \frac{\mu_i^2}{k}$$

$$\log(\mu_i) = F = n(X_{i,1} \dots X_{i,q})$$

In order to find the best explanatory variables, all combinations of independent factors were trialled, but never utilising collinear variables (e.g. temperature and photoperiod). Therefore, examples of trialled models are as follows:

$$N_i = \alpha + Temp_i + WL_i$$

$$N_i = \alpha + PP_i + \Delta WL_i$$

Following this, the effects of subject-specific (i) variables on the probability of tagged trout being first detected as autumn (AM_i) or spring migrants (SM_i) were explored. Binomial GLMs with a cloglog link function, due to asymmetry in the numbers of migrants and non-migrants, were constructed using combinations of the independent factors fish length (mm; Len_i), mass (g; Wgt_i) and Fulton's condition factor (K_i), but never with collinear variables (e.g. length and mass). The additional variables tag-site density (n·100m^{-2}, summer 2014; $Dens_i$), tag site distance from river mouth (km; $Dist_i$), and date of tagging

($Date_i$) were also analysed for migrants on the Deerness only. The binomial model is specified as follows:

$$AM_i \sim Bin(\pi_i)$$

$$E(AM_i) = \pi_i$$

$$var(AM_i) = \pi_i \times (1 - \pi_i)$$

$$cloglog(\pi_i) = F = n(X_{i,1} \ldots X_{i,q})$$

Examples of trialled models are as follows:

$$AM_i = \alpha + Len_i + K_i$$

$$SM_i = \alpha + Wgt_i + K_i + Dens_i + Dist_i + Date_i$$

Twelve Deerness fish, one a spring migrant, one an upstream migrant and 10 undetected, and two Villestrup fish, one a spring migrant and one undetected, were omitted from this analysis due to a lack of mass, and hence condition, records. All analyses were conducted in R 3.1.1 (R Core Team, 2014) with use of the MASS package (Venables & Ripley, 2002). Best models were chosen using the corrected Akaike's information criterion (AIC_c) minimisation (Burnham & Anderson, 2002), where models within $\Delta 6$ AIC_c were retained, provided they were not increasingly complex versions of more efficient nested counterparts (outlined by Richards, 2008).

For further examination, independent-sample *t*-tests were used to compare the net ground speed (km day^{-1}) of autumn and spring migrating individuals, while one-way ANOVAs, followed by post-hoc Tukey HSD analyses, were used to compare mean length, mass and condition factor of undetected individuals, autumn and spring downstream migrants, upstream migrants and residents (where relevant). An association between the date of spring detections and rate of growth was examined using Spearman's rank-order correlation tests for tagged migrant individuals captured during the March surveys. Chi-squared tests with Yates' continuity correction were also used to determine if the proportion of expected smolts recaptured in March and subsequently detected downstream differed by tag site, and if the proportion of Deerness downstream migrants reaching M1 (downstream-most PIT station) differed between autumn and spring. To analyse the diel periodicity of PIT detections, circular statistics were employed using the

'circular' package in R 3.1.1 (Agostinelli & Lund, 2013). For example, the circular mean, $\bar{\theta}$, is defined by:

$$\bar{\theta} = \begin{cases} \omega^{-1} arctan(A/B) & \text{if B} \geq 0 \\ \omega^{-1} arctan(A/B) + \pi & \text{if B} < 0 \end{cases}$$

using

$$A = \sum_{i=1}^{n} sin(\omega\theta_i) \quad \text{and} \quad B = \sum_{i=1}^{n} cos(\omega\theta_i)$$

where $\{\theta_i : i=1,\ldots,n\}$ are the observed cyclical data values and ω is a constant scaling the cyclical values to the range $(0,2\pi)$. For data representing the time of day $\omega = \pi/12$. The Watson-Williams test for the homogeneity of means could not be applied due to parameters of concentration for each data set being < 1 (i.e. a large degree of spread). Instead, chi-squared tests were used to compare the diel distribution of autumn and spring downstream migrant detections, using 2 hr bin sizes. Distributions were also compared between each consecutive month, but using 6 hr bin sizes to ensure expected counts were > 1. Whereas previous GLM analyses used only the details of a tagged individual's first detection, here multiple detections of the same individual were used if it was detected on more than one occasion, using a 1 hr filtering interval.

Chapter 3: Results – Fluctuating demographics and dispersal in the Deerness

3.1. HABITAT CLASSIFICATION

The habitat survey, based on protocols outlined by the Scottish Fisheries Coordination Centre (SFCC) collected information on juvenile trout habitats at six sites in the Deerness system dispersed over *ca.* 15 km of stream length. The predominant land use within 50 m of the bank top throughout the studied reach was agricultural, both arable and grassland, along with mixed broadleaf woodland. As such, canopy cover was equal to or exceeded 30% at all study sites. The average stream bank width of surveyed sections ranged from 2.6 to 5.4 m and decreased with distance from the river mouth (Table 3.1). Bed material was mostly pebble and cobble, with finer substrates in margins and sheltered areas and some larger boulders at all sites. Water depth ranged from 0 to >80 cm at all sites, with the deepest and largest (>50 m^2) holding pool found at T1. Sites T3 and T4 contained the largest proportions of shallow pebble and gravel (Table 3.1). Flow regimes were varied at all sites with a range of flow types from still to riffle. While water velocity was not measured directly, the flow categories give a suitable general description of the types of microhabitat available to juvenile trout. The proportion of pool habitat was equal to or exceeded 20% at five sites, while the proportion of faster flowing run and riffle habitat also exceeded 20% at five sites (Table 3.1). Bank cover suitable for fish refuge was predominantly provided by draping vegetation rooted on the bank, undercut banks and exposed roots at all sites, with some large rock also present at T1 and T5. Notably, the proportion of bank cover decreased with increasing distance from the river mouth on the Deerness, excluding site T5 which is found on the Hedleyhope Burn (Table 3.1). Damage due to bank collapse, erosion or trampling was minimal at all sites and of little major consequence to channel stability.

Table 3.1: Summary of habitat survey results conducted at each study site on the Deerness under the Scottish Fisheries Coordination Centre protocol (SFCC, 2007). Details of substrate and flow categorisations and abbreviations are given in Table 2.1. SM = Still Marginal, PO = Pool, GL = Glide, RU = Run, RI = Riffle.

	Distance from river mouth (km)	Bank Width (m)	Water Depth (%)				Predominant Substrate	Flow (%)					Bank Cover (%)
			0-20 cm	21-40 cm	41-80 cm	>80 cm		SM	PO	GL	RU	RI	
T1	4.2	5.4	42.5	7.5	15	35	CO	12.5	40	30	10	7.5	41.3
T2	6.2	4.6	37.5	23.75	25	13.75	PE-CO	8.75	21.25	33.75	21.25	15	25.6
T3	8.6	4.0	53.75	20	20	6.25	PE	12.5	17.5	21.25	32.5	16.25	18.8
T4	10.8	3.8	55	20	15	10	CO	20	22.5	20	30	7.5	16.3
T5	11.8	3.0	37.5	32.5	20	10	CO	7.5	27.5	27.5	20	17.5	27.5
T6	14.5	2.6	27.5	45	20	7.5	CO	12.5	20	32.5	25	10	12.5

3.2. POPULATION STRUCTURE

Preliminary ANOVA tests were used to compare the phenotypic characteristics of *tagged* individuals at each Deerness study site. The average length and mass of tagged trout differed significantly between sites (Length: $F_{5, 660} = 26.4$, $p < 0.001$; Mass: $F_{5, 648} = 23.3$, $p < 0.001$). Post-hoc Tukey analyses revealed tagged trout at T2 were significantly larger and heavier than those from all other sites at the $p < 0.001$ level (Fig. 3.1). Significant differences in condition factor were also observed ($F_{5, 648} = 5.4$, $p < 0.001$), with trout from T2 in better condition than those from T1 ($p = 0.004$) and trout from T5 in better condition than those from T1 ($p < 0.001$) and T6 ($p = 0.043$; Fig. 3.1).

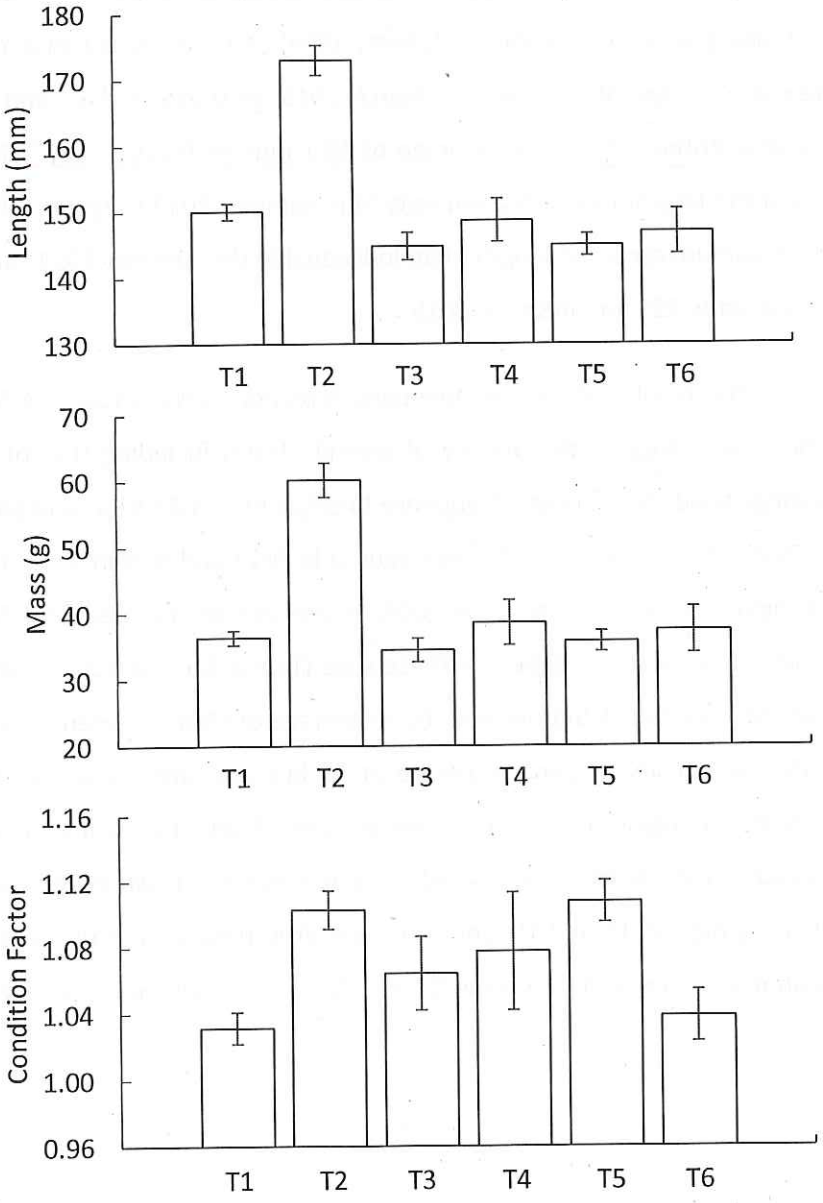

Fig. 3.1: The mean (± SEM) length, mass and condition of PIT-tagged trout in the Deerness by study site (n = 666).

The results of the November survey suggest a substantial proportion, 22.5%, of tagged and untagged parr morphotypes larger than 120 mm, sampled from five of the Deerness study sites, were spermiating and precociously mature males. Assuming a 50:50 sex ratio in the sampled juvenile population, this equates to 45% of all males.

Modal decomposition assessment (Bhattacharya, 1967) was completed on the lengths of all *untagged* fish caught at sites along the Deerness during multiple-pass depletion surveys in June-July 2014 and March 2015. This method discriminated three modes in the 2014 sample and two in the 2015 sample, each separated by values of $I_S > 2.0$ (Table 3.2; Fig. 3.2). Similar assessment by site could not be completed due to too few fish for the software to discriminate the modes. Assuming the length-frequency distributions of each age group were unimodal (Elliott, 1994), it is concluded that YOY fish in July 2014 grew an average of 15.7 mm by March 2015, or 0.075 % day^{-1} and age 1+ fish (second modal distribution) grew an average of 40.1 mm, or 0.119 % day^{-1} (Table 3.2; Fig. 3.2). A loss of the largest modal distributions from summer 2014 to spring 2015 was evident, with the maximum recorded length of an individual in the summer 2014 surveys being 297 mm, compared to 215 mm in spring 2015.

The results of the multiple-pass depletion surveys (Carle & Strub, 1978) give an estimated change in the density of juvenile trout, including that of specific age groups (distinguished by the length-frequency breakpoint of YOY trout and parr age 1+ and older, i.e. YOY ≤ 90 mm < parr), between June-July 2014 and March 2015. Overall trout density was highest at sites T1 and T5 in 2014, in line with the results of the habitat survey which estimated bank cover highest at these sites (Tables 3.1 and 3.3). While the density of YOY trout increased at all but one site, by an average of 88 % between summer 2014 and spring 2015, the density of parr decreased at all but one site, by an average of 49 %. These fluctuations largely offset each other at sites T3 and T4, such that overall trout density appeared quite stable. Interestingly, the proportion of fish cover was lowest at T6 and relatively high at T2 and T5, yet there was little reduction in the abundance of parr over autumn and winter at T6, while T2 and T5 became much more sparsely populated (Table 3.3).

Table 3.2: Output of the decomposition assessment using Bhattacharya's (1967) method for identification of modes in the length-frequency distributions of trout captured during triple-pass depletion surveys on the Deerness (sites T1-T6 combined) during June-July 2014 and March 2015.

Year	Mode	Mean Length ± SEM (mm)	Separation Index
2014	1	70.2 ± 0.4	-
	2	113.4 ± 0.7	2.55
	3	169.3 ± 1.1	2.50
2015	1	85.9 ± 0.4	-
	2	153.5 ± 1.5	2.78

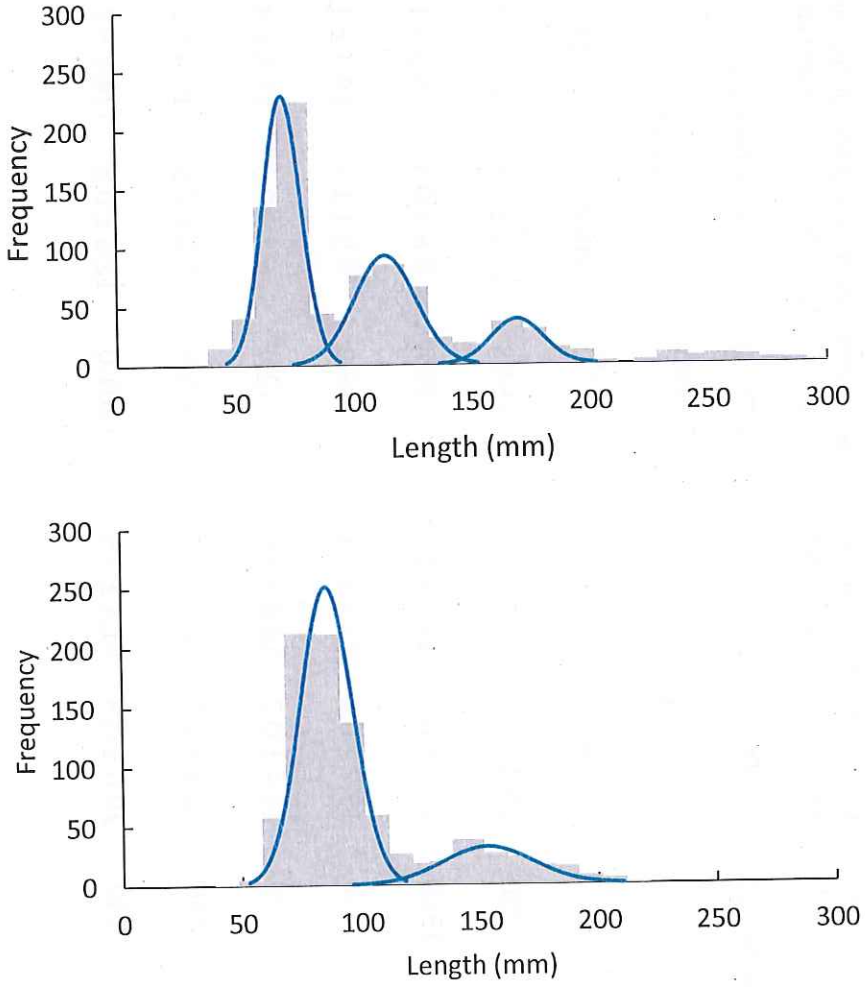

Fig. 3.2: Length-frequency distributions of trout captured during triple-pass depletion surveys on the Deerness, all sites combined, during June-July 2014 (top) and March 2015 (bottom), with the normal distributions of modes identified by decomposition analysis overlaid.

Table 3.3: Results of the triple-pass depletion surveys conducted in June-July 2014 and March 2015 used to estimate juvenile trout density. Specific age groups are distinguished by the length-frequency break point between YOY trout and parr (age 1+ and older) identified in the length-frequency decomposition assessment.

	Area surveyed (m^2)	Trout Density ($n \cdot 100m^{-2}$)		Δ Trout Density (%)	YOY Density ($n \cdot 100m^{-2}$)		Δ YOY Density (%)	Parr Density ($n \cdot 100m^{-2}$)		Δ Parr Density (%)
		2014	2015		2014	2015		2014	2015	
T1	790	29.4 ± 1.1	45.5 ± 2.3	+54.8	17.1 ± 0.8	30.5 ± 1.9	+78.4	12.0 ± 0.6	14.3 ± 1.0	+19.2
T2	1300	18.2 ± 0.6	13.5 ± 1.4	-25.8	8.8 ± 0.4	9.3 ± 1.3	+5.7	9.2 ± 0.3	3.7 ± 0.3	-59.8
T3	1050	19.2 ± 0.8	21.1 ± 1.6	+9.9	6.9 ± 1.7	19.1 ± 1.6	+176.8	12.2 ± 0.6	1.9 ± 0.6	-84.4
T4	520	16.4 ± 0.7	16.8 ± 3.0	+2.4	6.7 ± 0.3	15.5 ± 3.3	+131.3	9.5 ± 0.6	1.5 ± 0.1	-84.2
T5	440	28.8 ± 1.2	12.7 ± 2.5	-55.9	16.5 ± 0.9	10.4 ± 3.0	-37.0	12.2 ± 0.8	2.3 ± 0.4	-81.1
T6	340	20.6 ± 0.9	41.4 ± 2.5	+101.0	12.6 ± 0.5	34.4 ± 2.9	+173.0	7.7 ± 0.6	7.5 ± 0.4	-2.6

The estimated efficiency of triple-pass fishing episodes was always above 90% for YOY and parr in the Deerness during June-July 2014, averaging 98.1 % and 97.2 % across all sites, respectively (Fig. 3.3). In March 2015, the average efficiency of a triple-pass survey remained high for parr, at 98.4%, however that of YOY trout had decreased at all sites, to an average of 87.7%. From 2014 to 2015, the catchability of parr during a single-pass fishing episode decreased at sites T1, T2 and marginally at T4, while increasing in those remaining (Fig. 3.3). The catchability of YOY during a single pass was lowest in 2015 at all sites, particularly at T4 and T5, alongside a general increase in the density of this demographic from 2014 to 2015 (Table 3.3).

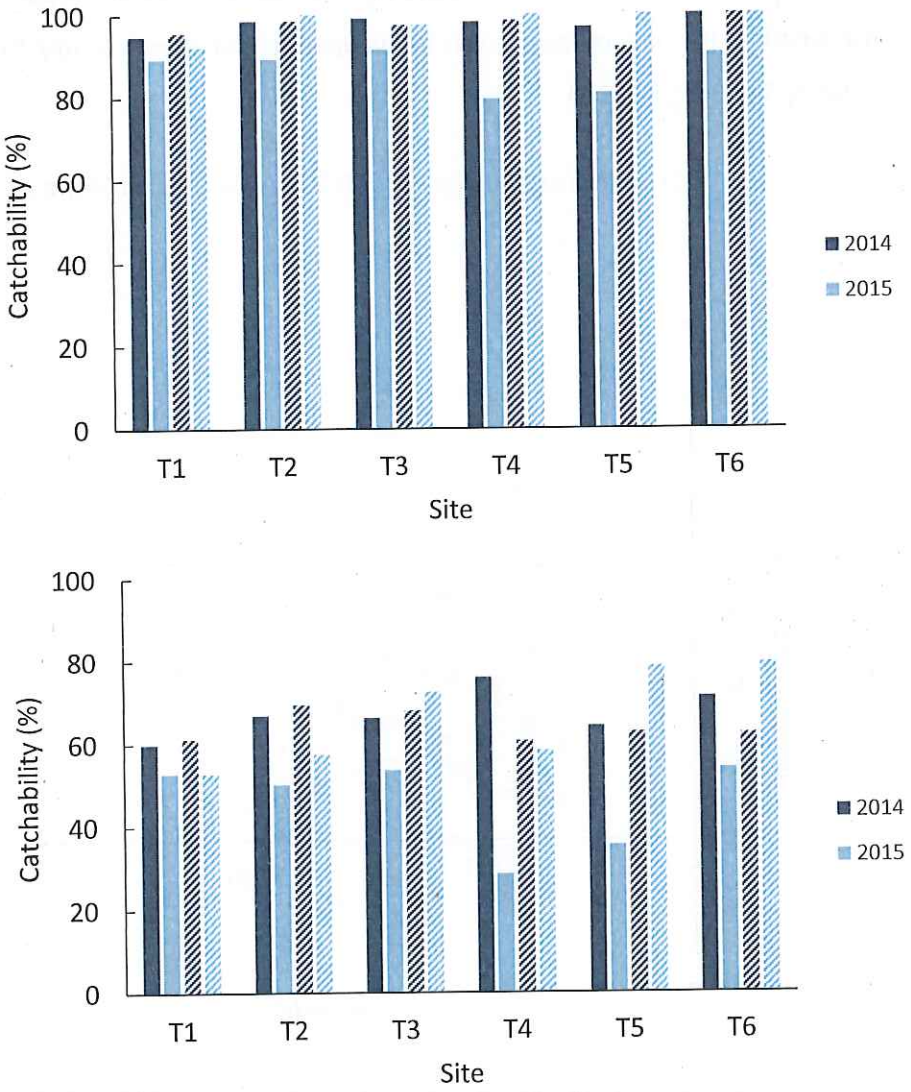

Fig. 3.3: Estimated catchability of YOY (solid bars) and parr (age 1+ and older) (patterned bars) during triple-pass (top) and single-pass (bottom) surveys in June-July 2014 and March 2015. Data displayed are calculated using the proportion of the estimated trout population (Carle & Strub, 1978) that are captured.

3.3. ESTIMATING GROWTH AND SURVIVAL

3.3.1. Growth

Regressions statistics revealed a significant relationship between fish mass at the time of tagging and rate of growth to March 2015 ($F_{1, 49}$ = 8.35, p = 0.006, R^2 = 0.15; Fig. 3.4):

$$Growth\ Rate\ [\%\ day^{-1}] = 12.8 - 0.181(Mass[g])$$

Conversely, no relationship was found between fish length and rate of growth to March 2015 ($F_{1, 49}$ = 3.67, p = 0.061, R^2 = 0.07; Fig. 3.5), but a significant negative linear effect of fish length at the time of tagging was found upon rate of growth to July 2015 ($F_{1, 17}$ = 4.68, p = 0.045, R^2 = 0.22; Fig. 3.5):

$$Growth\ Rate[\%\ day^{-1}] = 0.234 - 0.001(Length[mm])$$

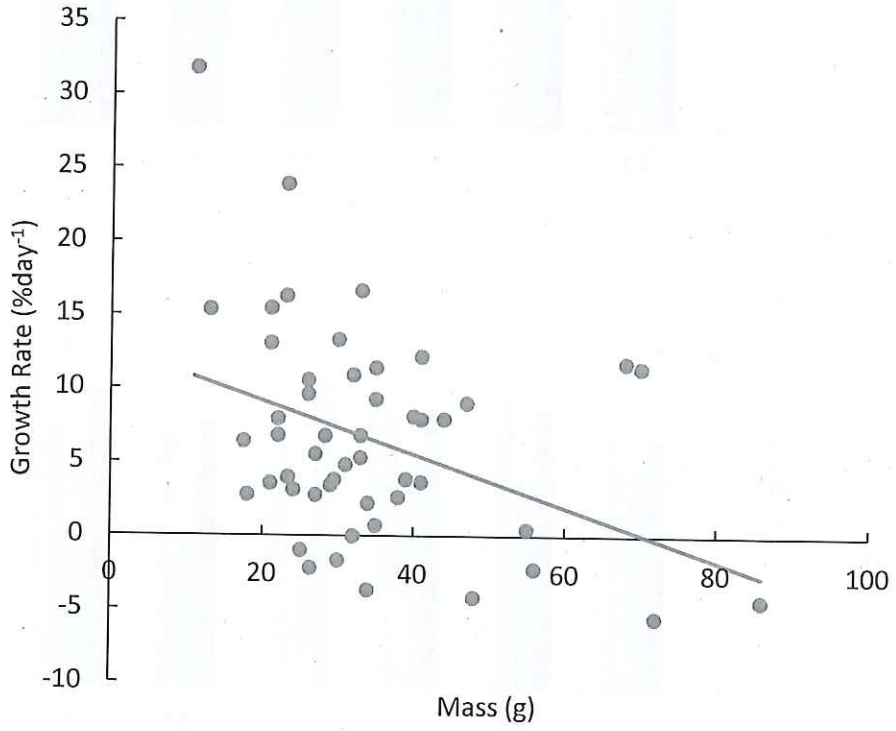

Fig. 3.4: The effect of mass at the time of tagging on growth rate to March 2015, measured for recaptured fish on the Deerness (sites T1-T6 combined).

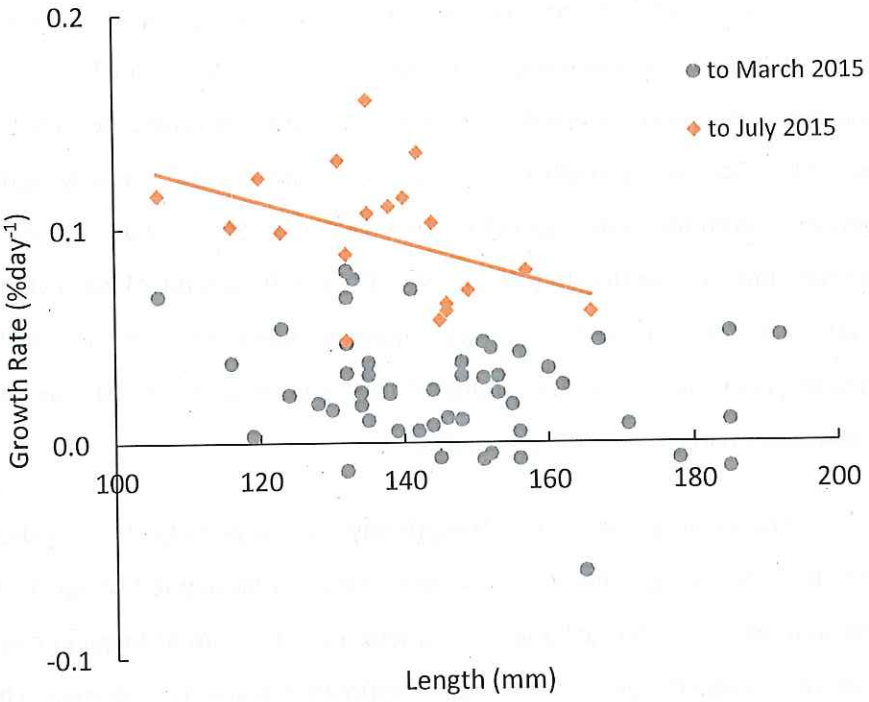

Fig. 3.5: The effect of length at the time of tagging on growth rate to March 2015 and July 2015, measured for recaptured fish on the Deerness (sites T1-T6 combined).

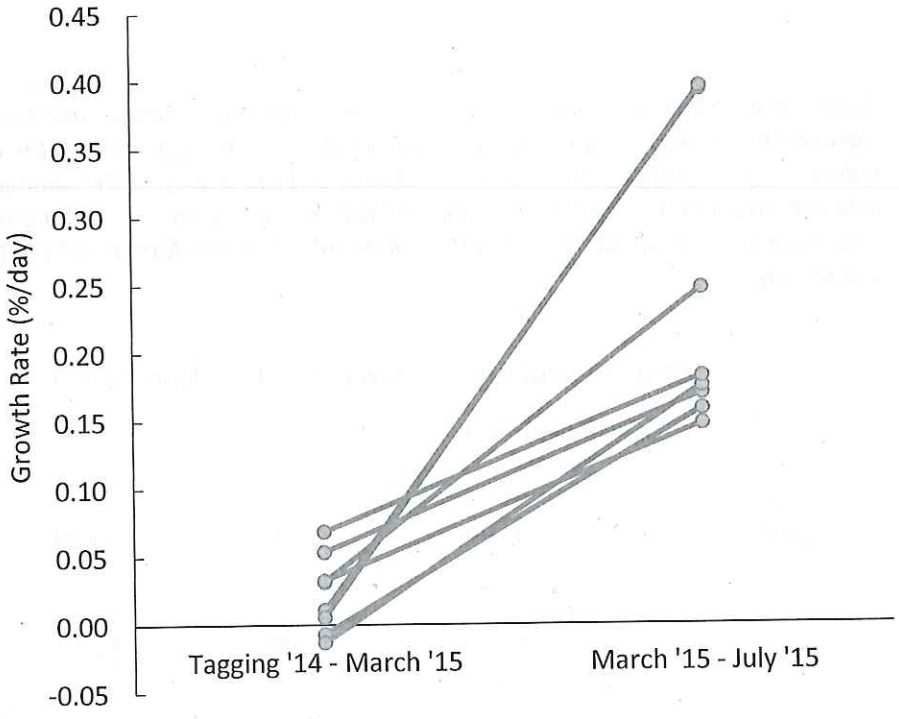

Fig. 3.6: Paired growth rates over autumn/winter and spring/summer for individuals recaptured in both the March and July 2015 surveys at sites T1-T6 on the Deerness.

Average growth rate for the period between tagging and March 2015 appeared lower than that between tagging and July 2015 (Fig. 3.5). To analyse this further a paired-samples t-test was conducted on individuals recaptured both in March 2015 and July 2015 (n = 8) to compare growth rate between capture events. A highly significant difference between autumn/winter growth rate (Mean ± SD = 0.023 ± 0.03 % day^{-1}) and spring/summer growth rate (Mean ± SD = 0.234 ± 0.10 % day^{-1}) was evident (t_7 = -5.28, p = 0.001; Fig. 3.6). No association was found between the rate of growth of recaptured individuals in March and the timing of their subsequent downstream migration (n = 17; Spearman's Rank: r_s = 0.006, p = 0.982).

The mean growth rate (%Length day^{-1}) of tagged age 1+ individuals recaptured in March 2015 (distinguished by the length-frequency breakpoint of age 1+ and 2+ groups in the summer 2014 Bhattacharya assessment, i.e. <150 mm at tagging) can be compared to that of untagged age 1+ individuals, estimated using the average change in length-frequency distribution over a similar time period. It was revealed that growth rate was markedly lower for tagged fish than for untagged fish (Table 3.4), by an average of 0.09 %day^{-1}. Given that the 95% confidence intervals for these values do not overlap, the difference can be said to be significant.

Table 3.4: Mean growth rate to March 2015 for tagged and untagged age 1+ trout, all Deerness sites combined, with 95% CI and N values presented. For tagged trout, the average value for individuals from tagging to recapture in March 2015 is displayed. For untagged trout, growth rate was calculated using the difference in mean lengths of age 1+ modal groups in the length-frequency decomposition assessments for June-July 2014 and March 2015 (difference in sample size shown).

	Mean Growth Rate (%Length day^{-1})	Lower 95% CI	Upper 95% CI	N
Tagged	0.029	0.020	0.038	55
Untagged	0.119	0.105	0.133	302 (2014) 149 (2015)

3.3.2. Survival

For analysis of survival probability during the summer of 2014 in MARK, goodness-of-fit tests confirmed that the Cormack-Jolly-Seber models adequately fit the data from each study site with a lack of overdispersion (Table 3.5: $p > 0.05$, C-hat < 2). Recapture probability was constrained to values displayed in Fig. 3.3 for parr in 2014, allowing estimates of apparent monthly survival to be calculated for all intervals between encounters. At sites T2, T4 and T5 model selection results favoured the more constrained model ($phi_{(.)}$) with time-constant survival probability (Table 3.6: AIC_c weight = 0.89, 0.75 and 0.79, respectively). Estimates of monthly survival varied by only 0.034 between these sites and averaged 0.73, although uncertainty increased with distance from the river mouth (Fig 3.6). At sites T1, T3 and T6 time-variant models ($phi_{(t)}$) were preferred (Table 3.6: AIC_c weight = 1.00, 0.92 and 0.53 respectively). Estimates varied substantially by interval at these sites, but all were highest during interval two, which generally represented the month of August, although intervals were not equal between sites. The highest and lowest probabilities of survival were estimated at 0.93 and 0.29, both for T3 during intervals two and three, respectively, while survival was lowest at sites T1 and T6 during interval one, representing July (Fig. 3.7). There was moderate support for simplifying the T6 model with time-independence (AIC_c weight = 0.47), producing a constant monthly survival probability, ϕ, of 0.65.

During the March depletion surveys, 50 of 643 individuals tagged prior to 12 September 2014 were recaptured, representing an apparent survival probability of 0.078 in the studied reaches, assuming no tag loss. This compares to an estimated survival probability over *ca.* 8 months of 0.081, when averaging and extrapolating the time-independent results from the MARK analysis (0.73^8).

Table 3.5: Goodness-of-fit test results for data from each study site, using full time variation in probabilities of both survival and recapture.

	χ^2	d.f.	C-hat	*p*
T1	7.18	4	1.80	0.127
T2	2.56	3	0.85	0.464
T3	4.16	3	1.39	0.245
T4	0.19	3	0.06	0.980
T5	1.51	4	0.38	0.825
T6	2.51	4	0.63	0.643

Table 3.6: Time-constant ($phi_{(.)}$) or time-variant ($phi_{(t)}$) model selection for estimates of apparent survival of juvenile brown trout in the Deerness during the summer of 2014. For each model the AIC_c, ΔAIC_c, AIC_c weight, number of parameters and deviance are reported.

	Model	AIC_c	ΔAIC_c	AIC_c Weight	No. of Parameters	Deviance
T1	$phi_{(t)}$	484.6	0.00	1.00	3	48.0
	$phi_{(.)}$	506.6	21.98	0.00	1	74.1
T2	$phi_{(.)}$	305.6	0.00	0.89	1	16.3
	$phi_{(t)}$	309.7	4.08	0.11	3	16.2
T3	$phi_{(t)}$	221.0	0.00	0.92	3	34.7
	$phi_{(.)}$	225.8	4.80	0.08	1	43.7
T4	$phi_{(.)}$	141.8	0.00	0.75	1	12.6
	$phi_{(t)}$	144.0	2.15	0.25	3	10.5
T5	$phi_{(.)}$	89.8	0.00	0.79	1	7.7
	$phi_{(t)}$	92.5	2.63	0.21	3	5.9
T6	$phi_{(t)}$	109.1	0.00	0.53	3	5.7
	$phi_{(.)}$	109.3	0.24	0.47	1	10.3

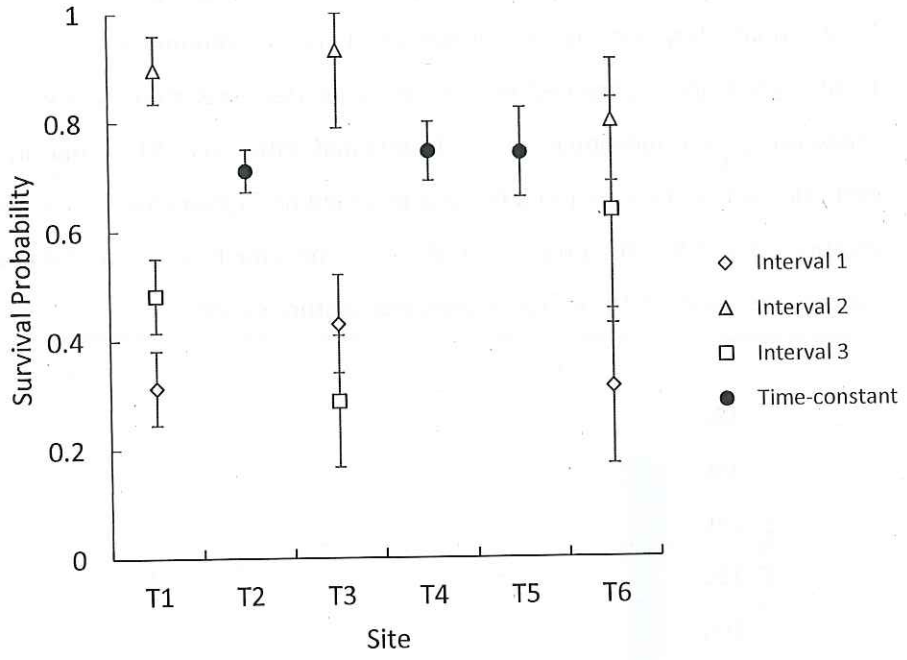

Fig. 3.7: Apparent monthly survival probability estimates ± SE for each study site on the Deerness. For sites T1, T3 and T6 models with time-dependent survival probability were favoured and estimates are presented for each time interval. In general, interval 1 represents late July, interval 2 mid-August and interval 3 late August to early September, however intervals were not equal between sites. Time-constant estimates of survival are presented for sites T2, T4 and T5.

3.2. SITE FIDELITY

A total of 330 fish were recaptured during single-pass surveys on the Deerness between late July and mid-September 2014. The maximum distance covered by any one trout tagged and recaptured within the same Deerness study site was 260 m, however many recaptured individuals (50.2%) remained within the 20 m zone in which they were first released, and the majority (83.0%) travelled no further than 60m from previous known locations (Fig. 3.8).. The proportion of tagged individuals recaptured during the single-pass surveys averaged 52.1% across all sites and capture events.

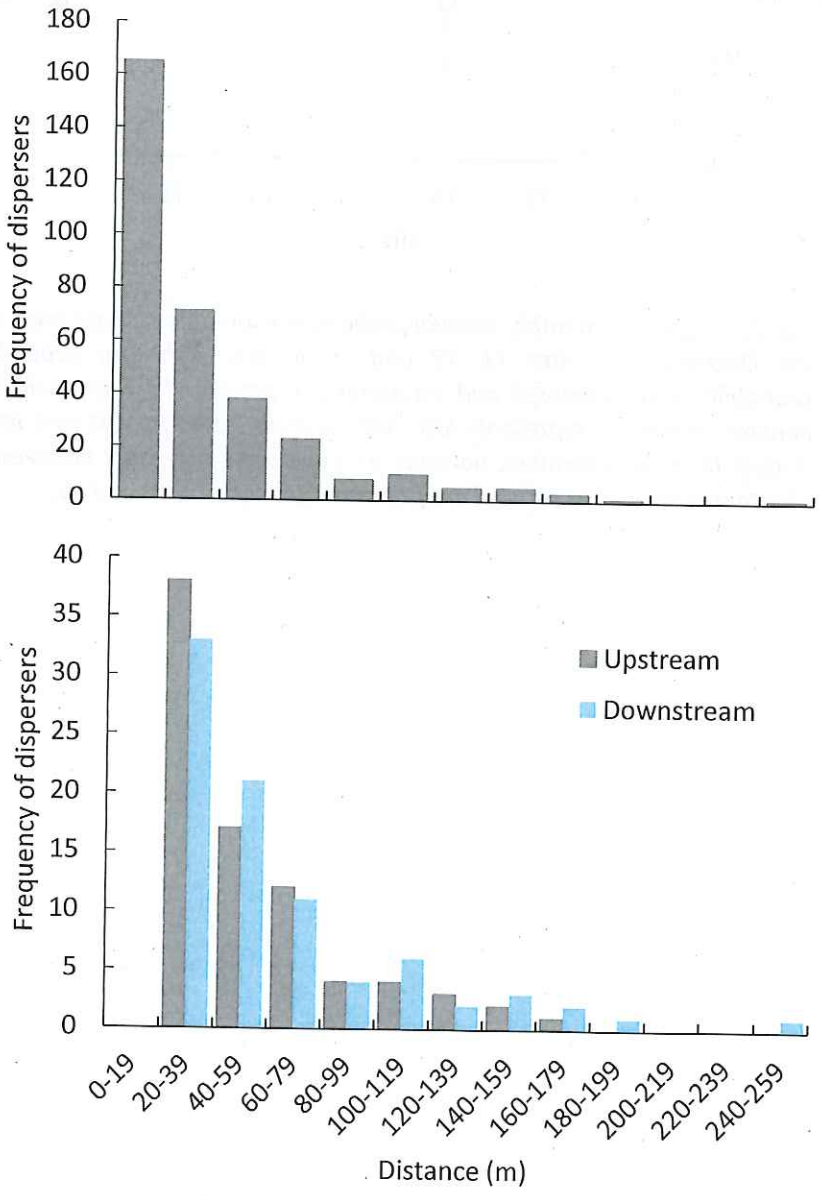

Fig. 3.8: Frequency distribution of the maximum longitudinal movements made by trout from a previous release site (top), with upstream and downstream movements separated (bottom), all study sites combined.

The probability, M, of moving a dispersal distance of D m was described by an inverse-power function using the inverse cumulative proportion of dispersers in each 20 m sample zone from the site of release (Bubb *et al.* 2004):

$$M = CD^{-n}$$

C and n are scaling constants. A highly significant negative relationship between ln$M$, both upstream and downstream, and ln$D$ was found (Upstream: $F_{1,7} = 82.7$, $p < 0.001$, $R^2 = 0.92$; Downstream: $F_{1,10} = 121.7$, $p < 0.001$, $R^2 = 0.92$; Fig. 3.9) under the equations:

$$\ln M \text{ (upstream)} = 7.25 - 2.26(\ln D)$$

$$\ln M \text{ (downstream)} = 7.22 - 2.21(\ln D)$$

No significant difference between the gradients of the two regression lines was found ($t_{20} = -0.18$, $p = 0.86$), meaning trout were equally likely to disperse upstream and downstream.

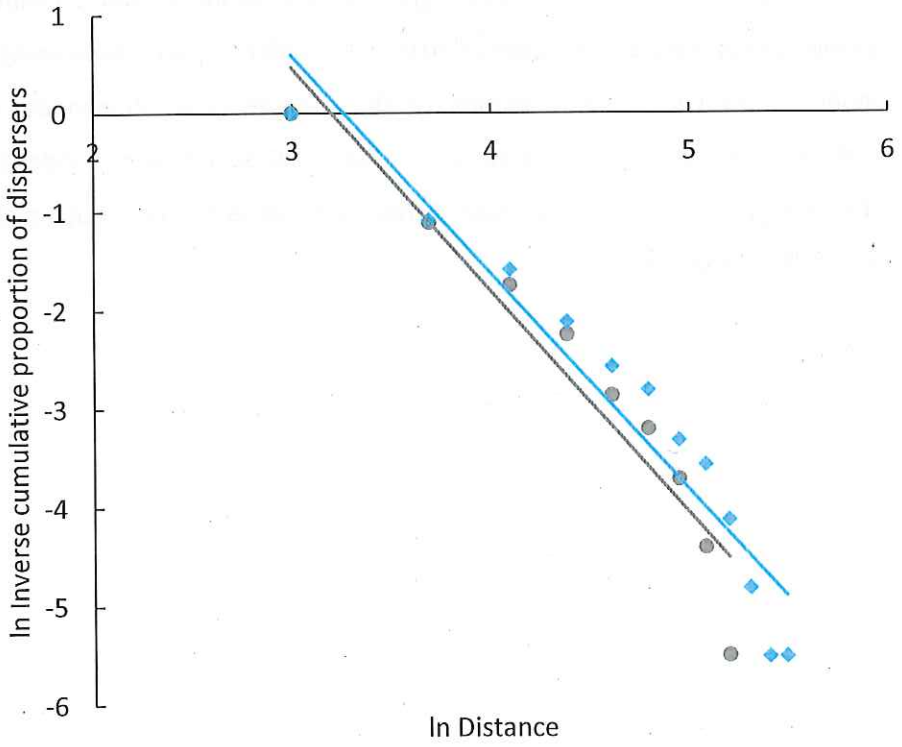

Fig. 3.9: Double-ln plot of the inverse cumulative proportion of dispersers in upstream (grey) and downstream (blue) directions from a previous known site of release.

Some evidence of large-scale dispersal (≥2 km) in summer 2014 was given by two individuals recaptured at a different study site to which they were tagged and released; one trout released at T2 was recaptured downstream at T1, and another released at T3 was recaptured upstream at T4. Neither were subsequently detected at any PIT monitoring station when installed in September and October, however the latter was again captured at T3 in November 2014. Also in November, an individual tagged at T5 was recaptured at T1, but was not detected at any PIT monitoring station. Two fish were captured at study sites downstream of their origin in March 2015, one of which was then PIT detected leaving the Deerness system. In July 2015, another trout had moved upstream from T3 to T4.

In summary, this chapter examined a number of indices of population dynamics in the Deerness. Tagged trout were of a similar size at each tag site, except at T2, where inhabitants were significantly larger. Length-frequency distributions of juvenile trout differed between seasons, with a loss of the uppermost mode in spring. This was reflected by a decrease in parr density at all but one tag sites, which contrasted an increase in YOY density at all but one tag sites. Fish size was positively correlated with growth across all seasons and rate of growth was highest during spring/summer. Estimates of monthly survival probability during summer 2014 were variable, particularly using time-dependent models, however an extrapolation of the average time-independent estimate closely matched the observed recapture rate in March 2015, indicating model efficiency. Finally, site fidelity was found to be high during summer 2014 for trout at all sites, although anomalies did occur.

Chapter 4: Results – Intrinsic and extrinsic factors affect phenology of migration

4.1. PHENOLOGY OF MIGRATION

Of the 666 Deerness trout, 140 (21.0%) were detected downstream of the site at which they were tagged and released, comprising 83 autumn migrants, 52 spring migrants and five individuals with activity spanning both periods (from here on labelled autumn migrants). Details by study site are given in Table 4.1. Notably, site T2 appears an outlier in the declining trend of proportions of migrants with increasing distance from the river mouth. Trout detected at M1 were assumed to have left the Deerness system, comprising 89 individuals in total (13.4%), 41 in autumn and 48 in spring. Migratory behaviour on the Deerness was observed throughout the period of study, with peaks of activity in October, November, March and May (Fig. 4.1). A further 35 individuals were labelled residents of M3, having been tagged within 260m of the monitoring site and detected at M3 only, and 11 were labelled upstream migrants from T1 to M3, all occurring in autumn and none of which were recorded leaving the stream.

*Table 4.1: Details of PIT tagging and telemetry results on the **Deerness** by study site, along with relevant statistics relating to PIT-tagged recaptures in March 2015. '% Migrated downstream' refers to the percentage of tagged fish in a reach that were recorded migrating downstream at one or more PIT stations; '% Recaptured residents' refers to the percentage of tagged fish in a reach that were recaptured in that same reach in March 2015, but were not detected at any PIT station, prior to or following the survey.*

	Distance from river mouth (km)	No. fish tagged	% Migrated Downstream	% Recaptured Non-migrants
T1	4.2	214	33.6	3.7
T2	6.2	99	10.1	6.1
T3	8.6	91	28.6	4.4
T4	10.8	55	18.2	7.3
T5	11.8	140	12.1	2.1
T6	14.5	67	7.5	11.9

In the River Villestrup, 195 of 490 tagged trout (39.8 %) were detected at the monitoring site and/or caught in the trap, comprising 49 autumn migrants, 136 spring migrants, and 10 individuals with activity spanning both periods (from here on labelled autumn migrants). The Villestrup trout did not display a distinct autumnal peak of activity, however low levels of migratory behaviour were sustained throughout autumn and winter months. Activity of spring smolts peaked in late March, with continued high levels of movement throughout April and early May (Fig. 4.1).

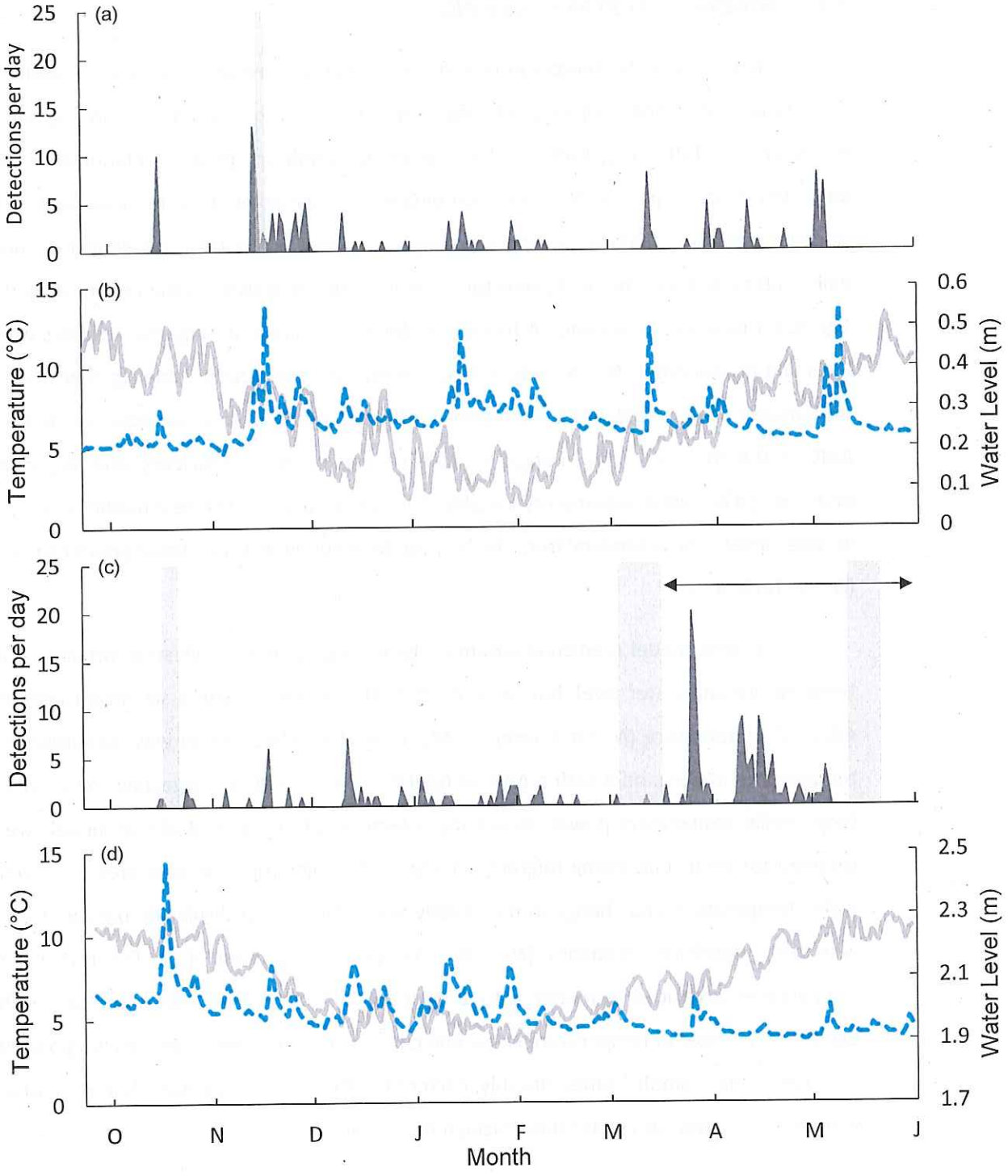

Fig. 4.1: Daily detection frequency of PIT tagged trout parr detected downstream of the site at which they were tagged and released on the Deerness (a) and Villestrup (c). Date of first detection only is displayed. Shaded regions represent periods of minimal or no detection efficiency due to PIT antennae / hardware malfunction. Individuals detected prior to 1 Feb were labelled autumn migrants and those detected from 1 Feb labelled spring smolts following published convention (Ibbotson et al. 2013). In addition, a downstream trap was operational from 18 March on the Villestrup, indicated by the arrow on panel (c). Average daily water temperature (solid lines) and average daily water level (dotted lines) are also displayed for the Deerness (b) and Villestrup (d).

4.2. GENERALISED LINEAR MODELLING

Mean daily water temperature and water level were retained in the best model ($N_i = \alpha + Temp_i + WL_i$; $\Delta AIC = 0$) for predicting daily detection frequency of autumn migrants in the Deerness (Table 4.2), both sharing statistically significant positive relationships with daily detection frequency. No other combinations of variables were retained under the selection criteria, reflecting their poor explanatory power. In contrast, the change in mean daily water level was the best predictor of spring migrant activity in the Deerness, with a significant positive relationship. A further model was retained utilising the variables water level and photoperiod ($N_i = \alpha + WL_i + PP_i$), however a greater ΔAIC value signified weaker explanatory power (Table 4.2). The removal of photoperiod from this model resulted in a ΔAIC of 0.8 ($N_i = \alpha + WL_i$), indicating little change in model efficiency and suggesting photoperiod is a weak explanatory variable. This is in contrast to the best predictor, change in water level, whose removal from the best model resulted in a ΔAIC value greater than six ($N_i = \alpha$; Table 4.2).

The best model predicting autumn migrant activity in the Villestrup retained both temperature and water level, but, in contrast to the Deerness, with a significant negative effect of temperature ($N_i = \alpha + Temp_i + WL_i$; Table 4.2). Photoperiod was substituted for temperature in the model with a ΔAIC of 0.9 ($N_i = \alpha + PP_i + WL_i$), suggesting the variables have similar explanatory power. Under the selection criteria, a total of five models were retained for predicting spring migrant activity in the Villestrup. The best predictors were water temperature and change in mean daily water level, both displaying positive trends with daily detection frequency ($N_i = \alpha + Temp_i + \Delta WL_i$; Table 4.2). The removal of temperature produced a model with a ΔAIC of 0.3 ($N_i = \alpha + \Delta WL_i$), indicating the explanatory power of temperature is low and change in water level on its own is a powerful predictor of daily smolt counts. Notably, each of the three remaining models also utilised a variable associated with water flow through the system.

Table 4.2: Generalised linear model outputs of migration phenology analyses. All retained models within 6 ΔAIC are displayed. Significant variables are in bold, with values for predictor variables representing coefficient estimates.

Model	AICc	ΔAICc	Df	Intercept	Water Level	Δ Water Level	Water	Photoperiod
Deerness Autumn								
1	202.3	0.0	4	**-12.00**	**33.30**		**0.24**	
Deerness Spring								
1	166.8	0.0	3	**-1.76**		**22.83**		
2	168.3	1.5	4	**-9.51**	**20.24**			**0.004**
3	169.1	2.3	3	**-5.84**	**17.35**			
Villestrup Autumn								
1	207.7	0.0	4	**-20.80**	**10.83**		**-0.34**	
2	208.6	0.9	4	**-18.23**	**11.02**			**-0.011**
Villestrup Spring								
1	311.7	0.0	4	**-1.87**		**27.04**	**0.20**	
2	312.0	0.3	3	-0.26		21.68		
3	316.1	4.4	4	-29.64	13.77			**0.004**
4	316.4	4.7	4	**-34.35**	**16.62**		**0.28**	
5	317.3	5.6	3	-17.57	9.10			

The best model describing autumn migrant tendency in the Deerness retained fish mass and tag site distance upstream as predictive parameters, both with significant negative correlations ($AM_i = \alpha + Wgt_i + Dist_i$ Table 4.3; Fig. 4.2). Three alternative models utilising combinations of length, condition, distance and date can be found in Table 4.3. Date of tagging displayed no significant relationship with autumn migratory tendency. The most efficient model predicting spring migration retained fish mass, condition factor and tag site distance upstream ($SM_i = \alpha + Wgt_i + K_i + Dist_i$). Mass and tag site distance shared significant negative relationships with probability of spring detection, while condition factor shared a positive relationship (Table 4.3; Fig. 4.2). Tag site distance was retained in all models for the Deerness, suggesting it is a strong predictor of migratory tendency for all downstream migrating juveniles, but particularly for spring smolts, given the higher coefficient estimates. This is supported by significantly more smolts (captured, inspected and classified in March 2015) than expected being detected originating from T1, the most downstream tag site, relative to sites further upstream (Chi-square: $\chi^2_1 = 6.18$, $p = 0.013$).

Autumn and spring migratory tendency in the Villestrup were best predicted by fish mass and condition, both sharing negative relationships in each scenario (e.g. $AM_i = \alpha + Wgt_i + K_i$ Table 4.3; Fig. 4.2). For the autumn migrants, mass was a particularly strong predictor on its own, given the removal of condition to produce a model with a ΔAIC of only 0.7 ($AM_i = \alpha + Wgt_i$). In similarity to the Deerness, fish length was retained in models with greater ΔAIC values, signifying weaker explanatory power.

Table 4.3: Generalised linear model outputs of migration tendency analyses. All retained models within 6 ΔAIC are displayed. Significant variables are in bold, with values for predictor variables representing coefficient estimates.

Model	AICc	ΔAICc	Df	Intercept	Length	Mass	Condition	Density	Distance	Date
Deerness Autumn										
1	487.4	0.0	3	0.26		**-0.032**			**-0.136**	
2	489.7	2.3	5	**4.29**	**-0.023**		**-1.86**		**-0.146**	0.006
3	489.7	2.3	4	**3.93**	**-0.022**		-1.42		**-0.137**	
4	491.3	3.9	3	**2.48**	**-0.022**				**-0.143**	
Deerness Spring										
1	340.7	0.0	4	-1.35		**-0.041**	**1.79**		**-0.178**	
2	341.0	0.3	3	**3.42**	**-0.029**				**-0.178**	
3	343.0	2.3	3	0.24		**-0.035**			**-0.164**	
Villestrup Autumn										
1	353.9	0.0	3	2.15		**-0.023**	-3.33			
2	354.6	0.7	2	**-1.21**		**-0.024**				
3	356.0	2.1	3	4.34	**-0.014**		**-4.19**			
4	358.4	4.5	2	-0.002	**-0.014**					
5	359.3	5.4	2	2.34			**-4.22**			
Villestrup Spring										
1	527.0	0.0	3	**4.70**		**-0.026**	**-4.42**			
2	532.6	5.6	3	**7.40**	**-0.017**		**-5.47**			

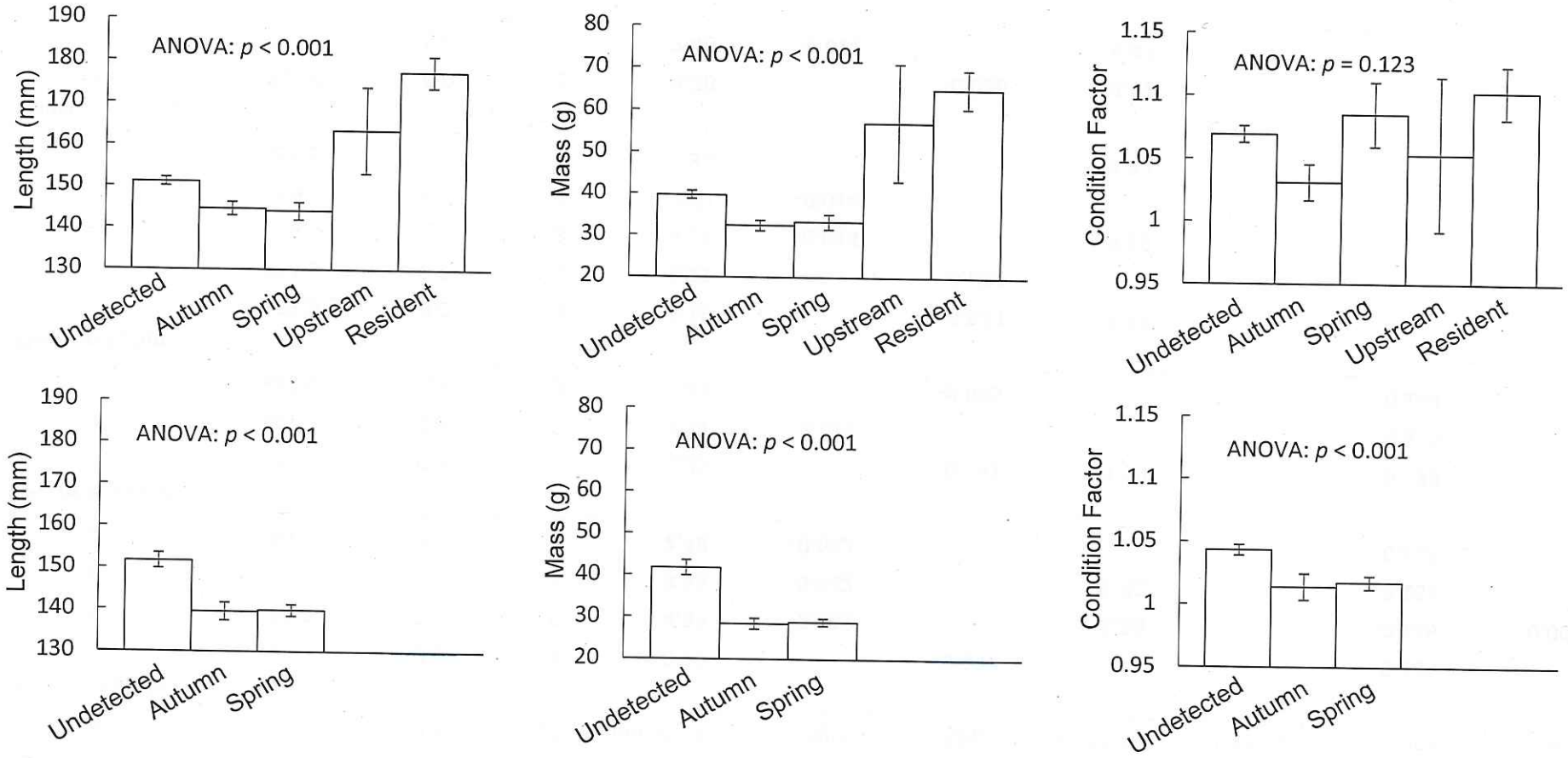

Fig. 4.2: The mean length, mass and condition factor at tagging (± SEM) of undetected trout, autumn downstream migrants, spring downstream migrants, upstream migrants and residents in the Deerness (top row) and the Villestrup (bottom row)

4.3. COMPARISONS OF MIGRATORY PHENOTYPES

There were significant differences in mean length (ANOVA: $F_{4, 661} = 16.7$, $p < 0.001$) and mass ($F_{4, 649} = 38.5$, $p < 0.001$) of migratory groups of individuals in the Deerness. Post-hoc comparisons employing the Tukey HSD test revealed resident trout at M3 were significantly longer and heavier at the $p < 0.001$ level than autumn downstream migrants, spring downstream migrants and undetected individuals, however no significant difference in length or mass was found between residents and upstream migrants (Length: $p = 0.358$; Mass: $p = 0.832$; Fig. 4.2). No difference in length or mass was found between autumn and spring migrants (Length: $p = 1.000$; Mass: $p = 0.999$), and while undetected individuals were significantly heavier than autumn migrants ($p = 0.024$), they were not longer ($p = 0.077$). Condition factor did not differ between migratory groups of trout in the Deerness (ANOVA: $F_{4, 649} = 1.8$, $p = 0.123$), however employing a *t*-test to compare only autumn and spring downstream migrants gave some evidence to suggest condition was greater in spring migrants ($t_{137} = 2.00$, $p = 0.048$; Fig. 4.2).

In the Villestrup, length, mass and condition factor differed significantly between migratory groups of individuals (ANOVA: Length: $F_{2, 487} = 11.7$, $p < 0.001$; Mass: $F_{2, 485} = 15.5$, $p < 0.001$; Condition: $F_{2, 485} = 8.8$, $p < 0.001$). Through post-hoc analyses, undetected trout were shown to be larger, heavier and in better condition than autumn (Legnth: $p = 0.004$; Mass: $p = 0.001$; Condition: $p = 0.009$) and spring downstream migrants (Length: $p < 0.001$; Mass: $p < 0.001$; Condition: $p = 0.001$), however autumn and spring migrants did not differ (Fig. 4.2).

Individual net ground speed of downstream migrants in the Deerness varied dramatically from less than 1 to 88 km day^{-1} throughout the study period, but on average, spring migrants travelled significantly faster (24.3 km day^{-1}) than autumn migrants (11.0 km day^{-1}) ($t_{127} = 3.82$, $p < 0.001$; Fig. 4.3). Additionally, downstream migrants were classified as stream 'emigrants' following a final detection at the most downstream monitoring site, *ca.* 700 m from the Deerness' confluence with the river Browney. A significantly greater proportion of spring migrants (84.6%) than autumn migrants (49.4%) became stream emigrants during the period in which they were first detected (Chi-square: $\chi^2_1 = 15.5$, $p < 0.001$). Five autumn non-emigrants were subsequently detected in the spring, four of which moved past M1 and likely emigrated the stream.

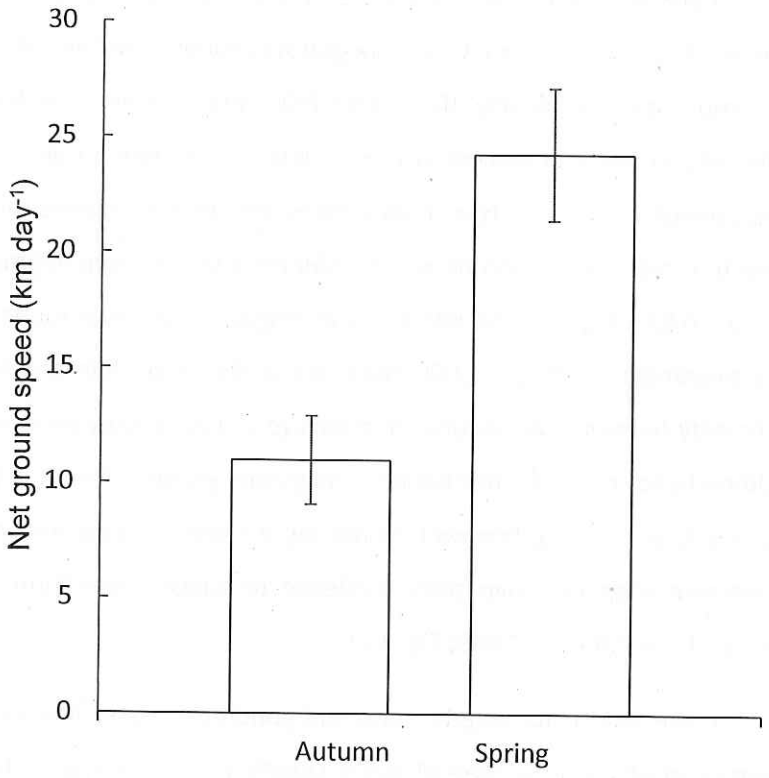

Fig. 4.3: The mean net ground speed (± SEM) of autumn and spring migrants in the Deerness

4.4. DIEL PERIODICITY OF MIGRATION

Applying circular statistics to the diel periodicity of PIT detections allowed a comparison of circadian distributions between seasons and months. Autumn and winter migrants were detected at an average time of 21:42, while spring migrants were detected at an average time of 21:54 (Fig. 4.4). The majority of migratory activity in autumn and winter fell between the hours of 17:00 and 06:00, while an additional peak of activity around 14:00 was present in spring. Variability in the timing of spring detections is illustrated by the location of the arrow tip in Fig. 4.4 – an arrow tip closer to the centre of the circle signifies a greater degree of spread. Using 2 hr bins, a significant association was found between time of year, autumn or spring, and time of detection (χ^2_{12} = 22.2, p = 0.036). Upon closer inspection, it is evident the mean times of detection during the months of October to April occurred between dusk and dawn, however that of May occurred during daylight. When comparing consecutive months using 6 hr bins, significant differences in the distribution of detection times occurred only between April and May (χ^2_4 = 30.7, p < 0.001; Fig. 4.4).

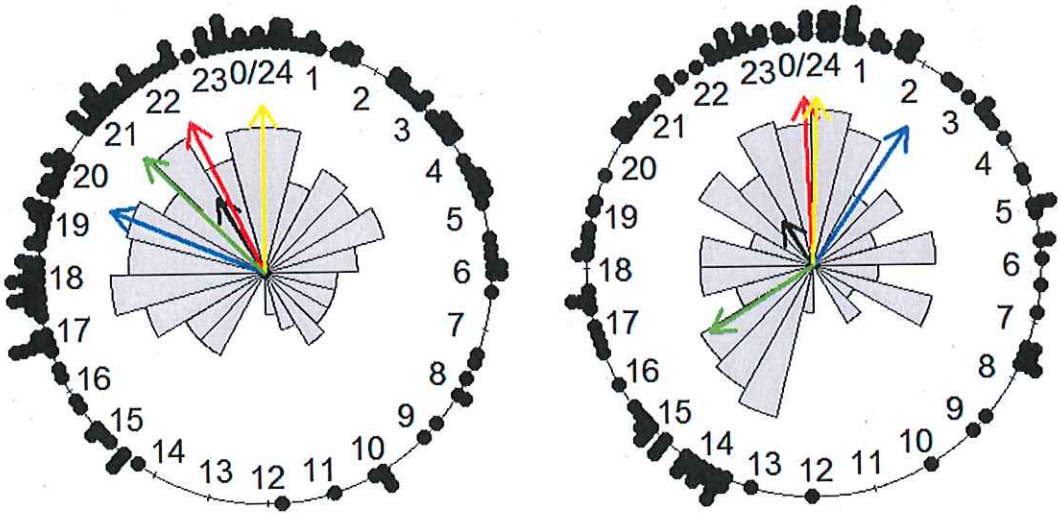

Fig. 4.4: Diel PIT detection frequency of autumn (left) and spring (right) downstream migrants, using a ≥ 1 hr interval filter for fish detected repeatedly at the same monitoring site. Black arrows represent diel mean values for the season. Blue, red, yellow and green arrows represent diel means for October/February, November/March, December/April and January/May, respectively. For scale, bar 0/24-1 represents 12 detections in autumn (left) and 11 in spring (right).

In summary, this chapter analysed factors driving the downstream migration of trout in different seasons and geographic locations. Detections of autumn migrants outweighed those of spring migrants in the Deerness, although a greater proportion of spring migrants than autumn migrants emigrated the study system. Autumn migration was also evident in the Villestrup, but to a lesser degree than in the Deerness. Probability of migration was enhanced by increased river discharge in each season and at each location, and positive effects of water temperature were found for Deerness autumn and Villestrup spring migrants. This is in contrast to Villestrup autumn migrants which responded negatively to temperature. Fish of a smaller size were more likely to migrate in both rivers, but autumn and spring migrants did not differ in size (at the time of tagging), although spring migrants were in better condition and migrated faster than autumn migrants in the Deerness. Probability of migration decreased in an upstream direction in the Deerness, although site T2 was an outlier in this trend. No effect of trout density on the probability of downstream migration was observed in the Deerness. Migration was largely nocturnal in the Deerness between the months of October and April, although a significant daylight peak of activity was observed in May.

Chapter 5: Discussion and Interpretation

This study is amongst the first to document the downstream migration of juvenile brown trout (*Salmo trutta*) over autumn, winter and spring, with temporal comparisons between seasons and geographical comparisons between two European locations. Chapter 3 gave a preliminary analysis of the population structure and dynamics of juvenile trout in the River Deerness before and during behavioural monitoring. The following chapter examined the results of PIT telemetry, a successful approach for the continuous, remote tracking of animal movements, in both the Deerness and River Villestrup, in order to quantify phenology of migration alongside investigating the potential factors regulating such migratory behaviour. A considerable degree of juvenile autumn migration was evident in both study systems, in contrast to the strong site fidelity observed during summer months in the Deerness. River discharge, fish size and proximity to the river mouth proved important as behavioural drivers. This final chapter provides a discussion and interpretation of data from all sources presented in Chapters 3 and 4, then considers potential management implications of key findings and offers recommendations for future research.

5.1. EFFECTS OF HABITAT ON TROUT DENSITY

The upper limit of juvenile fish abundance, or carrying capacity, is set by the availability of nursery and rearing habitat, aside from density-dependent factors, such as competition and predation that may function within this (Bjornn & Reiser, 1991). For river fish such as salmonids, temperature, productivity and water quality can regulate the distribution of individuals within a whole drainage system, while at specific locations, water velocity, depth, substrate and cover are important determining factors of fish presence (Armstrong *et al.* 2003). Throughout much of the Deerness riparian zone, native broadleaf trees regulated temperature through shading, also delivering leaf litter to support productivity, acting to stabilise the bank structure and buffering agricultural runoff. At a finer scale, it can be said that each Deerness study site offered a diverse array of stream microhabitats and flow regimes, beneficial to a number of juvenile trout life stages, given that with increasing age and size of parr, the amount of space required for feeding and refuge expands (Armstrong *et al.* 2003).

In more detail, the size of the substrate is important for juvenile rearing, with finer sediments supporting some aquatic invertebrates on which trout feed, while the interstitial spaces between larger gravel particles, cobbles and boulders provide cover from competitors and predators, and resting areas when water velocity is high. During winter, the availability of cover and refuge can be more important for survival than that of food, and therefore the carrying capacity of certain stream sections may change seasonally (Bjornn & Reiser, 1991; Armstrong *et al.* 2003). Brown trout are known to shift habitat to select coarser substrate in the autumn, relative to their size (Bjornn, 1971; Maki-Petäys *et al.* 1997). This does not, however, explain the large-scale redistributions (>2 km) of parr in the Deerness over autumn and winter, given that substrate composition was naturally varied throughout the study sites and river reach. Fish cover is considered very important for the abundance and overwinter survival of salmonids (Heggenes, 1996; Armstrong & Griffiths, 2001), and is also provided by deep water, surface turbulence, characteristics of bank structure, woody debris (Armstrong *et al.* 2003) and even ice (Linnansaari *et al.* 2009), allowing fish to inhabit areas otherwise unsuitable. For example, overwinter survival of juvenile rainbow trout (*O. mykiss*) was greater in stream sections with variable bank structure than in sections with more uniform habitat characteristics (Mitro & Zale, 2002). Older and larger trout generally occupy deeper, slower stream sections than smaller young-of-the-year (YOY) fish, which are often concentrated in stream margins (Cunjak and Power, 1986; Greenberg *et al.* 1996). This implies the availability of deep water can limit the abundance of ≥ 1+ parr, particularly in winter (Heggenes, 1996). In general, population dynamics in the Deerness support this notion, given the mostly limited availability of deep water and the reduction in abundance of parr between summer and the following March. Site T1 was the only site to experience an increase in abundance of parr from summer 2014 to early spring 2015, likely due to it having the greatest proportions of deeper water and available bank cover for concealment.

Some care must be taken when using fish densities as a measure of juvenile trout spatial requirements, with higher densities inferring smaller territories and better habitat quality. Van Horne (1983) gave several examples where species density and habitat quality are not positively correlated, for example due to intraspecific social interactions or food availability. This may not be wholly relevant to salmonids, given their territorial nature and reluctance to socially aggregate (Klemetsen *et al.* 2003), however interspecific competition for refuge can also be intense (Harwood *et al.* 2002*a*). Furthermore, higher fish densities in pools may simply reflect more available volumetric space, rather than a particular habitat

preference (Bjornn & Reiser, 1991). In the Deerness, changes in the population density of specific age groups were widely variable by study site, irrespective of available fish cover, which may indicate complex interactions of additional population-regulating factors. Further investigation into the specific micro- and mesohabitat utilisation of parr at each Deerness study site would be required to fully assess its impact upon seasonal trout abundance.

5.2. ESTIMATING FISH GROWTH AND SURVIVAL

The pattern seen in the length-frequency distribution of Deerness trout in July 2014 is typical of populations with multiple cohorts, being multimodal and with each mode resembling a normal distribution about a mean length (King, 1998). Hence, one can have confidence in the length-frequency break points of specific age-groups distinguished by the Bhattacharya assessment. The length-frequency distribution of trout in March 2015 was more unusual, in that individuals >200 mm were not represented, possibly indicating mortality, emigration or poor catchability. Seasonal differences in fish behaviour may affect the probability of capture, including a reduction in diurnal activity during colder months (Heggenes, 1996) or increased refuge, such as under overhanging banks (Armstrong *et al.* 2003). Negative relationships between age or body size and overwinter mortality have been reported (Letcher *et al.* 2002; Carlson *et al.* 2008), possibly due to susceptibility to predation or a lack of suitable habitat, in which case the loss of large individuals in the Deerness may not be surprising. Alternatively, others describe positive relationships between salmonid size and mortality (Johnston *et al.* 2005), or a lack of evidence to suggest any size-dependent mortality (Lund *et al.* 2003). Importantly, the increase in population size of YOY trout from July 2014 cannot be attributed to recruitment (too early for 2015 fry emergence), and suggests rates of immigration may have exceeded emigration for this age group. Based on this inference, it should not be assumed that the change in density of older parr can be attributed solely to mortality, since net movement may also be responsible for changes in population size, resulting in directional dispersal away from capture and release sites. Deerness PIT detected migrants cannot fully account for the marked reduction in abundance of large trout by March 2015, especially given the negative relationship between fish size and detection probability. Therefore, at least some local movement outside tagging sites during autumn and winter seems a plausible conclusion,

likely related to the availability of overwintering refuge, in view of potential seasonal shifts in mesohabitat suitability (Bjornn & Reiser, 1991; Armstrong *et al.* 2003).

The apparent increase in abundance of YOY trout to March 2015 could also be explained by a change in their probability of capture. When using electrofishing methods, catchability increases with size of the fish (Borgstrøm & Skaala, 1993; Peterson *et al.* 2004), implying the ratio of small YOY to large, older parr was underestimated in July 2014 (approx. 1:1), compared to 2015 (approx. 3:1). Yet, in the present study, catchability of YOY trout in a triple-pass fishing episode decreased from an average of 98% to 87% from July to March. This may be partly attributed to a change in environmental conditions from summer low-flow conditions to spring medium-flow conditions, since variation in water temperature, depth and turbidity can cause capture efficiency to fluctuate (Speas *et al.* 2004). Moreover, the utility of depletion fishing methods in accurately assessing fish abundance has been questioned (Peterson *et al.* 2004), and with more YOY fish having attained a size large enough to capture in March, a higher density could have saturated electrofishing sampling gear and reduced efficiency (Speas *et al.* 2004).

Theoretically, growth rate decreases with age and size of the fish (Elliott, 1994), as was observed for tagged trout in the Deerness both to March and July 2015, with some individuals experiencing negative growth during winter (Jonsson & Jonsson, 2011). Conversely, analysis of the length-frequency distribution of untagged fish revealed the growth rate of 1+ parr exceeded that of YOY trout to March 2015. Mean length values computed in the length-frequency decomposition assessment could, however, be biased, if catchability of the smallest individuals in 2014 was low, therefore underestimating the average increase in length of YOY trout. Alternatively, the separation of modes naturally decreases with age, size and reduced growth rate (King, 1998), meaning the lengths of 1+ and 2+ trout in 2015 could have been overlapping and risking overestimating the average increase in length of 1+ parr. Bimodal size distributions have been observed within a single cohort of brown trout, where the upper modal group, in the autumn, was expected to smolt the following spring (Glover *et al.* 2003), but fish age was not directly quantified in the Deerness. Ultimately, the length-frequency distributions can only act as guide and extensive fish scale or otolith analyses would be required to thoroughly examine age-specific rates of growth.

For Atlantic salmon of similar size to the Deerness trout, Larsen *et al.* (2013) found no significant effect of tagging with 23 mm PIT tags on fish survival or growth in captive fish

experiments. Additionally, while tag retention was not monitored in this study, previous studies on juvenile salmonids report minimal tag loss, such as 0% for Atlantic salmon larger than 100 mm FL tagged with 23 mm PIT tags (Larsen *et al.* 2013) and <1% for age-0 Atlantic salmon (Gries & Letcher, 2002). In the present study, the growth rate of untagged 1+ trout was significantly greater than that of tagged 1+ trout, by a factor of almost four, however a number of elements could have biased this result. A possible overestimation of the average increase in length of untagged 1+ parr to March 2015 due to poor separation of length-frequency modes has already been discussed. Secondly, the growth rate of untagged 1+ parr was estimated for fish measuring between 90 and 150 mm FL in 2014, whereas tagged 1+ parr measured between 120 and 150 mm FL at tagging. Hence, given the negative relationship between size and growth rate (Elliott & Hurley, 1995; Jonsson & Jonsson, 2011), the average value for untagged parr would be expected to be greater. Thirdly, the first multiple-pass depletion survey of untagged parr was conducted earlier in the season than PIT tagging, when summer growth rates were expected to be high (Elliott, 1994; Jonsson & Jonsson, 2011). Seasonal variation in growth was evident for Deerness trout, with the spring/summer growth rate in 2015 exceeding that of autumn/winter. As such, many of the untagged fish, but not the tagged fish, were sampled during a period of high summer productivity, and changes in size would have reflected this.

Nevertheless, the reported difference in growth rates is a concern and could indicate a detrimental effect of the tagging, handling and recapture process on fish welfare. Jepsen *et al.* (2015) have identified the need for a clearer distinction between capture and handling effects from telemetry tagging on subsequent performance outcomes (growth, natural mortality etc.), as yet largely unresolved. The behavioural results of this study should, therefore, be taken with caution, although comparisons between autumn and spring migratory behaviour should still be valid, if the effects of tagging were consistent across phenotypes.

Survival was predicted to be high for trout in the Deerness during summer months. The Cormack-Jolly-Seber (CJS) analyses in MARK distinguished two types of apparent monthly survival for trout in the Deerness during summer 2014; time-dependent and time-independent. Time-dependent values were highly variable and differed somewhat by site, likely indicating a complexity of biological and physical, site-specific factors affecting survival, whereas time-independent values remained relatively constant. The estimates of monthly survival described in Chapter 3, excluding those for interval two at sites T1, T3 and T6, were considerably lower than those reported for adult and juvenile brown trout in

summer (Olsen and Vøllestad, 2001; Lund *et al.* 2003; Carlson *et al.* 2008), which do not fall below 0.85. The values for the time-independent estimates are, instead, similar to those reported by Carlson and Letcher (2003) for 1+ trout in spring and summer. It is important to recall that the CJS model parameters represent estimates of *apparent* survival and therefore underestimate the true value of survival. This is due to the difficulty in separating death from permanent unavailability for capture, for example as a result of emigration (Horton & Letcher, 2008). The degree to which apparent survival reflects true survival is dependent on the match between study design and the species biology, for example the size of the study area (60 m stream sections above and below each Deerness in-stream structure) relative to the typical home range size (Horton & Letcher, 2008). As predicted, the mark-recapture experiment revealed a high proportion, 83%, of recaptured trout remained within 60 m of previous known locations during summer 2014. This indicates a high degree of site fidelity, and the interpretation of model parameter estimates should, therefore, be appropriate, although low estimates for monthly survival could reflect some movement of fish out of the study area during that time interval.

Survival estimates for salmonids often vary between years (Needham *et al.* 1945), between seasons (Elliott, 1993; Letcher *et al.* 2002; Carlson & Letcher, 2003) and within seasons (Smith & Griffith, 1994) although evidence does not always support temporal variation (Lund *et al.* 2003; Carlson *et al.* 2008). In the present study, probability of survival to March 2015 was estimated at 0.081, using an extrapolation of the average time-independent value over eight months, and hence assumed no seasonal variation in mortality. In the literature, it is generally regarded that winter incurs severe costs to increase the mortality of juvenile trout (Needham *et al.* 1945; Cunjak *et al.* 1998), for example due to the depletion of energy reserves (Hutchings *et al.* 1999) or limited winter habitat availability (Whalen *et al.* 1999). As such, the value quantified for survival to March 2015 would likely be overestimated. Alternatively, some studies have failed to observe a winter bottleneck in survival (Olsen & Vøllestad, 2001; Lund *et al.* 2003), and in fact suggest lowest survival for juvenile trout in spring (Elliott, 1993) or autumn (Carlson & Letcher, 2003), due to episodic events such as droughts and floods. Consequently, it is possible the present study's estimate for overwinter survival could be lower than the true value.

The accuracy of the CJS survival estimate to March 2015 can be validated using the measured probability of recapture of *tagged* individuals over the same sample area in March 2015, which equated to 0.078. These values are remarkably similar, confirming the reliability of the modelling approach for tagged individuals and giving reason to oppose

seasonal variation in mortality in the Deerness. The slight overestimation of the CJS model is likely attributed to increased rates of either emigration or mortality over autumn and winter, in comparison to summer values from which the estimate is derived, or a combination of both. Given that the PIT telemetry confirmed significant emigration of juvenile trout from the study sites over autumn and winter, this may suggest rates of autumn and winter mortality in the Deerness remained similar to those in summer. This is not necessarily unexpected, since self-sustaining populations should be adapted to local annual environmental fluctuations (Carlson *et al.* 2008). From another perspective, the probability of survival of *untagged* parr was 0.488, derived from the average change in population density of parr across all Deerness sites. This value is within the ranges reported by Needham *et al.* (1945) and Carlson and Letcher (2003) for overwintering, but far exceeds that estimated by the CJS modelling and recapture surveys, therefore suggesting a high degree of local movement and population shuffling into and out of the study areas.

5.3. MIGRATION VERSUS DISPERSAL

Extensive autumn downstream migrations, as well as spring smolt downstream migrations were evident in juvenile trout populations in both the Deerness (north-east England) and the Villestrup (Jutland, Denmark). Over 1.5 times the number of spring smolts were observed active between the months of October and January in the Deerness, with those leaving the system during autumn-winter representing 46 % of all downstream migrating juveniles in the study period. This provides quantitative evidence of the protracted overwinter nature of the downstream migratory behaviour, broadly similar to that of the Marine Institute (2014), which states numbers of autumn migrating juveniles in the Burrishoole catchment, Ireland, have fluctuated between 18 % and 57 % of the total annual juvenile downstream migrant count, since 1982. Incidence of migration was predicted to increase with proximity to the marine environment, due to a reduction in migration costs, and probability of downstream migration was found to be higher for trout in the Villestrup, which flows directly into a brackish fjord. Yet incidence of autumn migration was lower in the Villestrup (25% of the total juvenile migrant count) than in the Deerness, but remains higher than that reported by Jonsson and Jonsson (2009*b*) in Norway. In general, the recognition of an alternative juvenile downstream migratory phenotype is growing in a number of systems internationally. The results of the present study indicate the behavioural phenomenon is more widespread than previously assumed

and the potential contribution of these individuals to overall adult recruitment must be acknowledged.

The results of the mark-recapture experiment confirmed strong summer site fidelity for juvenile brown trout in the Deerness. This is further illustrated by substituting values into the power function (Bubb *et al.* 2004). For example, the probability of a fish achieving a dispersal distance of 1 km equated to < 0.001 in either longitudinal direction. While the greatest dispersal distances were observed in a downstream direction, no statistical evidence was available to suggest directional dispersal. In contrast, dispersal of salmonid parr is usually considered to occur in a downstream direction (e.g. Solomon & Templeton, 1976). A common bias of mark-recapture studies is the inability to monitor individuals moving out of the study area, often episodically (Gowan *et al.* 1994; Bolland *et al.* 2009). In the present study, the recapture of fish at different sites to which they were tagged and released, including two in summer 2014, highlights such difficulties in estimating the probability of large-scale dispersal. Furthermore, the return of one of those individuals to its original site of capture could suggest a large home range, over greater than 2km of river length, possibly indicating a poor match between study design and species biology (Horton & Letcher, 2008). Interpretation of mark-recapture studies can be further limited by low proportions of recaptures (Cunjak *et al.* 2005). In the present study, the summer recapture surveys sampled 52%, on average, of the tagged population, compared to a measured average catchability of 65% for parr in one single-pass fishing in 2014. Marking and handling does not appear to affect probability of capture after a 24-hr recovery period (Mesa & Schreck, 1992; Peterson *et al.* 2004), and hence this reduced recapture rate is likely a result of mortality or dispersal out of the study area. Importantly, however, capture efficiencies greater than 35 % are considered relatively high (Peterson *et al.* 2004) and these results represent a population majority (>50%), suggesting the degree of site fidelity in summer outweighs that during autumn and winter, also supported by the results of the March recapture surveys and PIT telemetry.

The distinction between dispersal and migration in salmonids is not always clear, for example, Crisp (1993) described movements of juvenile trout from a natal stream habitat as dispersal, including spring peaks of activity which are characteristic of the smolt migration. Migration is generally regarded as a recurrent movement between different macrohabitats (Dingle, 1996), while dispersal is a permanent, non-directional movement away from a natal home range (Howard, 1960). It, therefore, seems reasonable to label Deerness and Villestrup stream emigrants as 'migrants', given their transition to a main

river (Deerness) or brackish fjord (Villestrup) environment. Nevertheless, in the Deerness it is not possible to rule out longer distance dispersal as the mechanism responsible for some of the stream emigrants, which could breed in the Browney or Wear, but the concerted nature of the autumn movement suggests it could be part of the downstream migration cycle (whether potamodromous, anadromous, or a mixture). Continued PIT monitoring to record the return migration of fish of known origin in these systems would be needed throughout the upstream spawning migrations of the forthcoming years to conclusively ascertain the proportion of emigrants undergoing a true migration.

5.4. ENVIRONMENTAL REGULATORS OF MIGRATION TIMING

The environmental factors regulating the phenology of downstream movement of salmonid smolts have been well studied, in particular the behavioural responses to water temperature, flow and light (e.g. Jonsson, 1991; Aarestrup *et al.* 2002; Aldvén *et al.* 2015). It was predicted that trout in the Deerness and Villestrup would respond positively to temperature and water level, but stimuli for migration differ in their importance geographically between river systems and temporally between years (Hembre *et al.* 2001), acting to predict favourable oceanic conditions and maximise survival of migrants (McCormick *et al.* 1998). This study suggests that water level, which directly relates to river discharge, had the greatest positive influence on *autumn* migrant movement in both the Deerness and Villestrup, in accordance with Youngson *et al.* (1983) and Holmes *et al.* (2014). This is not surprising, given that high water velocity offers fish an opportunity to move rapidly downstream whilst minimising the energetic costs of migration, and high turbidity may offer greater protection from predators (Hvidsten & Hansen, 1989). Moreover, previous studies have noted the rate of downstream migration of brown trout and Atlantic salmon smolts is positively correlated with water velocity (Aarestrup *et al.* 2002). The change in average daily water level was a better predictor of movement of *spring* migrants in both the Deerness and Villestrup. This suggests smolts in both systems are particularly receptive to dynamic fluctuations in the hydrograph, similar to Carlsen *et al.*'s (2004) conclusions that migrating juveniles can anticipate floods. Importantly, all models retained in Table 4.2 utilised an environmental variable associated with river discharge, suggesting it is a central migratory stimulus for both populations.

The retention of additional environmental variables in models predicting the phenology of migration indicate other important migratory stimuli in the Deerness and

Villestrup. It may be expected that the probability of migration should decrease during the coldest and shortest-day periods, since salmonid activity and swimming performance is limited during cold winter conditions (Graham *et al.* 1996). As predicted, autumn migrants in the Deerness and smolts in the Villestrup responded positively to temperature, analogous to results obtained by Jonsson and Ruud-Hansen (1985). Smolt activity in the Deerness was better predicted by increasing photoperiod than temperature, which is known to regulate physiological changes associated with the parr-smolt transformation (Jonsson, 1991; McCormick *et al.* 1998; Björnsson *et al.* 2011). Contrary to expectations, the probability of autumn migration in the Villestrup shared a significant negative relationship with temperature. Jonsson & Jonsson (2002) also noted an increase in migration tendency with decreasing autumn temperature in the River Imsa, Norway, although fish up to 550 mm long were trapped and adult sea trout were not well distinguished from juveniles (size analysis, split only as greater or less than 300 mm). Other studies reporting increased migrant activity at cold temperatures are usually associated with ice melt (Hesthagen & Garnås, 1986; Carlsen *et al.* 2004). One possibility for the observed Villestrup pattern is that peak flows may have coincidentally occurred with low temperatures in winter, demonstrating a degree of behavioural independence with regard to seasonal variables. Also, the Villestrup is spring-fed, meaning temperatures are comparatively more stable to those of the Deerness. The relative importance of temperature, photoperiod and river discharge as migratory triggers may fluctuate between years (Jensen *et al.* 2012; Aldvén *et al.* 2015) and depending on precipitation and rate of temperature change. Longer-term studies in either system could, therefore, reveal inter-annual variability in the combined effect of environmental cues.

Trout migrations in the Deerness were predominantly crepuscular or nocturnal from October to April, in agreement with previous studies on salmonids (Jonsson, 1991; Moore *et al.* 1995; Aarestrup *et al.* 2002; Antonsson & Gudjonsson, 2002; Ibbotson *et al.* 2006). Nocturnal behaviour during the winter is thought to function in predator avoidance, particularly from endothermic predators whose energetic responses are not constrained by low temperatures (Thorpe *et al.* 1994; Moore *et al.* 1995; McCormick *et al.* 1998). Toward the end of the smolt migration season, migration activity in the Deerness became increasingly diurnal, in agreement with previous studies (Thorpe & Morgan, 1978; Greenstreet, 1992; Ibbotson *et al.* 2006). This seasonal shift has been attributed to increased water temperature, independent of photoperiod (Thorpe *et al.* 1994; Greenstreet, 1992), allowing quicker responses to predators. The present observations also

give reason to suggest high temperatures stimulated daytime migration in Deerness trout smolts.

Migration is closely adapted to environmental conditions, in particular water flow and temperature, and its timing influences survival during the transition to a new environment (McCormick *et al.* 1998). With projections of rapidly warming temperatures and more frequent extreme weather episodes, i.e. floods/droughts, the phenology of salmonid spring smolt migrations is predicted to advance, condense over a shorter time period and experience less annual variation (reviewed in Jonsson & Jonsson, 2009*a*). This has been confirmed using multi-decade surveys for multiple salmonid species (Kennedy & Crozier, 2010; Kovach *et al.* 2013; Otero *et al.* 2014). However, fears of phenological mismatching with peak marine productivity are allayed by stable population dynamics (Dahl *et al.* 2004; Kovach *et al.* 2013). There has been little discussion regarding the possible effects of climate change on the prevalence and survival of autumn migrants, however Holmes *et al.* (2014) propose an increased fitness advantage of autumn migration in unstable, unproductive natal stream habitat. Should an increase in precipitation and flow variability occur over autumn and winter, we may expect more fish to descend to sea over this time (Jonsson & Jonsson, 2009*a*).

Responses by migratory fish to environmental change have wider relevance with respect to aquatic ecosystem structure. Migration provides a valuable ecosystem service, including a seasonal flow of nutrients between different freshwater and marine habitats (Chapman *et al.* 2011), but variation in migration phenology can cause dramatic changes to trophic cascades. For example, the seasonal migration of zooplanktivorous cyprinid fish from temperate lakes has been modelled to drive zoo- and phytoplankton population dynamics, ultimately influencing the growth of submerged lacustrine macrohpytes (Brönmark *et al.* 2010). The value of autumn salmonid downstream migration in terms of freshwater or marine trophic dynamics and food web structure remains unclear, but continued climate warming and increasingly frequent environmental extremes could cause greater variability in migration timing, with unforeseen consequences. It is difficult to predict how the stability of aquatic and terrestrial populations will be influenced, but determining the degree of trout life history variation, with respect to autumn migration, over gradients of habitat stability and growth potential, for example over latitudinal, stream-order or long-term temporal variations in temperature, would be beneficial to fishery management and ecological theory (Homes *et al.* 2014). Such research could enable

identification of particularly vulnerable salmonid populations or freshwater ecosystems to environmental change or anthropogenic impacts such as flow abstraction.

5.5. STUDY SITE AND PHENOTYPIC DETERMINANTS OF MIGRATION TENDENCY

The probability of an individual juvenile trout conducting autumn or spring migration past fixed points on the Deerness decreased significantly in an upstream direction, or with decreasing proximity to the marine environment, as predicted. Ibbotson *et al.* (2013) proposed that a re-distribution or shift of autumn migrating Atlantic salmon parr in a downstream direction was responsible for similar findings, rather than a targeted migration. Given that migratory behaviour in the Deerness is strongly regulated by variable river discharge, one explanation for this may be to consider the potential disturbance caused by environmental events such as high autumn-winter flows. The motivation to defend a territory can increase with the residence time of a fish (Johnsson and Forser, 2002; Harwood *et al.* 2003). Therefore, high flows may disrupt territorial behaviour and initiate a re-establishment of dominance hierarchies, promoting the downstream displacement of subordinate individuals. While this may hold true for autumn-winter migrants, is it unlikely to be the case for spring smolts in the Deerness pursuing marine migrations, but for which there was a reduced probability of detection from tag sites further upstream. Moreover, there appears no trend in the percentage of recaptured residents with distance upstream (Table 4.1), which would be expected if migration tendency decreased in an upstream direction (Bohlin *et al.* 2001). It is therefore suggested a cumulative increase in mortality probability exists with increasing distance upstream for both autumn and spring migrants, for example due to anthropogenic obstruction during migration (Gauld *et al.* 2013), greater energetic costs or exposure to predators (Blackwell *et al.* 1998; Bohlin *et al.* 2001).

In early studies it was hypothesised that anadromous salmonid juveniles migrate at the first opportunity after reaching a threshold size (Elson, 1957; Fahy, 1985), yet for brown trout, smolt length has been shown to vary from <100 mm to >200 mm within the same Norwegian river system (Økland *et al.* 1993). Further investigation has revealed fast-growing individuals smolt younger and at a smaller size than their slow-growing counterparts (Forseth *et al.* 1999). Contrary to expectations, both in the Deerness and Villestrup, autumn and spring migratory tendency were negatively affected by body mass at tagging, which was always a better predictor than body length. This may be

counterintuitive, considering migration and post-migration survival is thought to be positively size-dependent (Bohlin *et al.* 1993), for example risk of predation decreases with size (Skov *et al.* 2010). Nevertheless, this finding suggests migrating juveniles in these river systems were fast-growing. Such individuals have high energetic demands and have less proportional energy available for growth than slow growers (i.e. more energetically constrained), which could explain why they seek alternative niches at a smaller size (Forseth *et al.* 1999). The timing of smolt migration for individuals recaptured in March did not correlate with body size, contrary to other observations (Jonsson *et al.* 1990; Bohlin *et al.* 1993; Jensen *et al.* 2012), however the sample size was small. Unexpectedly, in the Deerness (autumn migrants) and Villestrup (autumn and spring migrants) migratory tendency was negatively correlated with fish condition at tagging. Migration has been described as a biological response to adversity (Taylor & Taylor, 1977), and low condition could result from adversity in the form of poor growth opportunities. Notably, the optimal size at migration could be lower than the size range of individuals sampled, i.e. <120 mm, such that some of the tagged trout, especially males, may have been maturing. This is particularly convincing when considering that PIT tagged parr at site T2 were significantly larger, but less likely to migrate.

Some studies find autumn migrants to be significantly larger than spring migrants or residents of the same year-class, possibly indicating constrained habitat availability for faster-growing individuals or achievement of a high energy store status (Huntingford *et al.* 1992; Holmes *et al.* 2014). Alternatively, dominance and size may be positively correlated (Harwood *et al.* 2002*b*), and thus smaller individuals more likely to migrate when competition for overwintering refuge intensifies. Neither of these hypotheses are supported by the present study's results, since the size of autumn and spring migrants did not differ at the time of tagging in either the Deerness or Villestrup, as also found by Ibbotson *et al.* (2013) for Atlantic salmon. However, in the Deerness, spring migrants were of better condition than autumn migrants and autumn and spring migratory tendencies shared opposed relationships with individual body condition. This could be a result of competition, such that subordinate individuals with lower body condition were displaced by their dominant counterparts, either preferentially leaving a low-growth potential environment or forced out of overwintering habitat (see also: Keeley, 2001). Notably, one limitation of remote monitoring is the lack of information regarding fish size or condition at the time of migration. The results of the present study, along with Holmes *et al.* (2014) and Ibbotson *et al.* (2013), are based on the assumption that size at the time of tagging is an

accurate predictor of future physiological characteristics. There is some evidence to suggest first year growth of salmonids can predict future migratory behaviour (Jonsson & Jonsson, 1993), although a combination of PIT telemetry and periodic trapping of migrants could provide more detailed information on the growth of autumn versus spring migrants and thus their positions in a dominance hierarchy.

Migration in brown trout can be regulated by food availability (Wysujack *et al.* 2008), therefore autumn migrants could result from a competition-induced lack of resources for subordinates. Moreover, high trout density has a greater detrimental effect on the growth of small individuals (Jenkins *et al.* 1999), however no evidence was found to suggest the density of parr at each Deerness tag site could predict the proportion of autumn migrants. Migration as a result of competition is reflected in many non-salmonid species, for example in blue tits, *Cyanistes caerulus*, (Nilsson *et al.* 2008) and red deer (Mysterud *et al.* 2011), however care must be taken when using size or condition as indicators of competitive ability, since behavioural syndromes are also key to establishing dominance hierarchies (Ward *et al.* 2004).

Upstream migrants in the Deerness, characteristic of precocious parr maturation (McCormick *et al.* 1998), were, on average, larger than downstream migrants, suggesting stream residency. All remained in the stream during this study, although they may emigrate in the following years. Male parr maturation has been positively correlated with condition (Bohlin *et al.* 1994), which may explain why migratory tendency in the Villestrup decreased with increasing condition. Precocious parr are predominantly males and the anadromous emigrants' sex ratio is typically heavily skewed towards females (Klemetsen *et al.* 2003), but fish sex was unknown in this study, although a substantial proportion of tagged and untagged parr morphotypes larger than 120 mm, sampled on the Deerness in November 2014, were spermiating males. Cheap molecular methods for the sexing of juvenile salmonids from tissue samples are now available (Quéméré *et al.* 2014) and will aid sex-specific interpretation of movement patterns in parr morphotype salmonids in the future.

5.6. ECOLOGICAL SIGNIFICANCE AND MANAGEMENT IMPLICATIONS OF AUTUMN MIGRATION

An autumnal overwintering habitat shift to deeper, slower water is commonly reported for salmonids on a micro- to meso- habitat scale (Huusko *et al.* 2007) and may explain why approximately half of autumn migrants detected in the Deerness, although

travelling at least 2 km downstream from their sites of capture and release, were not observed emigrating from the river. Macrohabitat shifts are less common (but see Bjornn, 1971), but are likely necessary when overwintering habitat in the natal stream is unsuitable (Huusko *et al.* 2007). Why, then, should only a proportion of Deerness and Villestrup trout emigrate the streams during autumn and winter? A reduction in stream carrying capacity, resulting in intense intraspecific competition for resources and the expulsion of some individuals (Riley *et al.* 2008), may be responsible (Bjornn & Reiser, 1991; Armstrong *et al.* 2003). Similarly, in the River Frome, Atlantic salmon autumn migrants were more common from larger channels, likely where availability of overwintering refuge was low, relative to the size of the juvenile population (Ibbotson *et al.* 2013).

In several cases, autumn-winter downstream-migrating parr morphotypes are referred to as 'presmolts' with the implication that they are destined to go to sea (McGinnity *et al.* 2007; Ibbotson *et al.* 2013), however in the Deerness their migration strategy, i.e. anadromy or potamodromy, was unknown (though both migration forms do occur in the Wear catchment [M. Lucas, pers. comm.]). The Deerness catchment is characterised by mild, oceanic climates and frequent flow elevations following rainfall, possibly accounting for the large and prolonged 'autumn' downstream migration. It is highly likely that a substantial proportion of Deerness stream emigrants overwintered in the main River Wear rather than exiting immediately to sea. In contrast, migrants in the Villestrup are assumed to enter the brackish Mariager Fjord soon after passage through the PIT monitoring station, located a short distance upstream of the river mouth. They can therefore be labelled 'presmolts', since a return migration to freshwater is essential for reproduction.

Autumn migrant parr are assumed to have low gill $Na^{+}K^{+}$-ATPase activity as observed for autumn-emigrating Atlantic salmon juveniles (Riley *et al.* 2008), although no such studies have explored the salinity tolerance of autumn-emigrating trout parr. This could potentially cause osmoregulatory stress, but salmonid parr have been known to reside in estuarine environments (Cunjak *et al.* 1989; Pinder *et al.* 2007) and theoretically they could remain in the river outlet and outflow region. In the Deerness, the absence of an immediate physiological stressor in the main river may explain why incidence of autumn migration is particularly high. Direct translocations of autumn migrant salmonids into full strength seawater have not been successful (Riley *et al.* 2008), but it would be more valuable to determine the range of salinities and temperatures to which juvenile autumn emigrants are exposed and their survival in relation to their physiological readiness for

seawater transition. Acoustic telemetry, microchemistry or scale reading (to show freshwater vs. seawater growth) of recaptured spawners would be needed to describe these processes for individuals of known origin in either river system.

Questions regarding the ecological significance of autumn migration of juvenile salmonids remain, including whether, in some cases, the behaviour can be labelled a true migration. Increased plasma thyroxine levels in Atlantic salmon autumn migrants are suggestive of a real, physiologically mediated migration (Riley *et al.* 2008; Zydlewski *et al.* 2005), although it must be noted that changes in environmental stimuli, such as river turbidity, have also shown to induce such hormonal surges (Specker *et al.* 2000). The behavioural motivations of juvenile Atlantic salmon autumn and spring migrants may differ, since autumn-migrating parr are not physiologically adapted for seawater entry (Riley *et al.* 2008). In the present study, Deerness spring migrants travelled at a greater net ground speed, with values similar to those obtained by Aarestrup *et al.* (2002) for radio tagged trout smolts, and were more likely to become stream emigrants than were autumn migrants. While antennae malfunction over several days during a major spate in November 2014 may be partially responsible for a lack of autumn detections at the most downstream monitoring site, these results give reason to suggest the movements of Deerness autumn individuals were not exclusively marine-targeted.

It is suggested the autumn-migratory phenotype represents an important avenue within the migration continuum concept (Cucherousset *et al.* 2005; Dodson *et al.* 2013; Boel *et al.* 2014), such that juveniles make a plastic decision as to the season of downstream migration, dependent on environmental and physiological factors relating to individual fitness. A diversity of migratory phenotypes likely provides a selective advantage in unpredictable or fluctuating environments (Villar-Guerra *et al.* 2014), however requires more informed management of Atlantic salmon and brown trout populations, especially regarding fish passage and water abstraction. For example, it is common practice to mitigate the impoundment effects of dams or to screen water intake structures only during peak migration (smolt) season (Turnpenny & O'Keeffe, 2005). The results of this study indicate mitigation should also target downstream migrating parr, or 'presmolts', outside of the smolt period, particularly during autumn and winter peak flows.

Partial migration is taxonomically diverse and variability in migration timing is commonly reflected in non-salmonid species. For example, intense interference competition between shore crabs, *Carcinus maenus*, in the nursery habitat can stimulate

mass migrations of juveniles to potentially unsuitable habitats (Moksnes, 2004), and overwintering migrations in some birds can be highly unpredictable, dependent on population densities and seed crops (Newton, 2010). Migrants provide an ecological link between discrete habitats and influence biodiversity at local and global scales, but are increasingly vulnerable to environmental change, the rate of which varies across regions. Understanding the drivers of partial migration and how organisms make use of alternative habitats offers ecologists unique information on life history evolution and species adaptation. Perhaps the behavioural plasticity of partial migrants, such as the brown trout, will serve to buffer some populations from anthropogenic stressors (Chapman *et al.* 2011). The present study was atypical in its use of two separate migratory populations as independent replicates, but ultimately, future studies of partial migration will benefit from longer-term, metapopulation or community comparisons using advanced technology, which will enable more generalist behavioural models and driving mechanisms to be proposed. Understanding the contribution, or recruitment, of different migratory phenotypes to adult life history strategies is a significant challenge facing population monitoring and regulation. Should climate change induce greater variability in the seasonal timing of migration, this will become increasingly important in order to ensure the successful protection, restoration and longevity of brown trout populations, other salmonids, and partial migrants as a whole.

5.7. CONCLUSIONS

To conclude, this study provides quantitative evidence for considerable autumn and winter downstream migration in juvenile brown trout in the rivers Deerness and Villestrup, contrasting the strong site fidelity observed in the Deerness during the summer months. Analyses of Deerness trout population dynamics also implied a high degree of autumn/winter local redistribution, likely due to seasonal shifts in mesohabitat use. Correlative information was presented on factors regulating autumn/winter migration behaviour, to parallel the wealth of knowledge concerning spring smolt migration. Notably, migrants in both study systems responded positively to increased river discharge and migration tendency decreased with fish size. Probability of migration increased with proximity to the marine environment, likely due to reduced risk of mortality. Deerness spring migrants were in better condition, were more likely to become stream emigrants and travelled faster than autumn migrants. Hence, different behavioural motivations for autumn/winter and spring migrants were proposed, specifically an autumnal habitat shift versus a marine targeted migration, respectively. The limitations of repeat sampling and mark-recapture methods in monitoring fish movement were discussed, including poor recapture rates and an inability to monitor large-scale dispersal. On the contrary, the extensive PIT dataset highlighted the utility of biotelemetry in accurately assessing the incidence and phenology of migration and in enhancing our understanding of behavioural ecology.

These results emphasise the highly diverse array of overwintering habitats and the dynamic behavioural nature of the brown trout, which should influence more informed conservation and management plans, particularly given the species' importance in recreational, commercial and subsistence harvesting. Ultimately, an in-depth evaluation of the temporal and geographical variability of the extent of autumn migration is needed, along with further studies concerning the sex ratio, genetics, survival and subsequent reproduction of autumn migrant individuals. This will be necessary in understanding the evolutionary mechanisms responsible for an alternative migratory strategy and the role of an autumn-winter migratory phenotype in the recruitment of sea-migrating and potamodromous adult salmonids.

Appendix I: Standard terminology and descriptions of brown trout (*Salmo trutta*) life stages.

Term	Definition*
Alevin	Post egg-hatching stage with dependence on yolk sac as a source of nutrition.
Fry	Juvenile fish having dispersed from the redd and feeding independently of the yolk sac.
Parr	Juvenile fish with scales and camouflaging vertical bars (parr marks).
	0+ parr/young-of-the-year (YOY) = less than one year old
	1+ parr = one year or older, but less than two years
	2+ parr = two years or older, but less than three years
	etc.
Smolt	Migratory juvenile trout. Loss of parr marks, silvered colouration, darkened fins.
Finnock/Whitling	Small anadromous trout in first year at sea.
Adult brown trout	Sexually mature, freshwater-resident trout.
Adult sea trout	Sexually mature, anadromous trout.
Kelt	Spawned-out or spent migratory trout, until it re-enters seawater or shows re-growth on scales.

**Adapted from Allan and Ritter (1977). Similar definitions also apply to the corresponding life stages of Atlantic salmon,* Salmo salar.

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